Simone Maganuco\*, Cristiano Dal Sasso\*\*
&
Giovanni Pasini\*\*\*

# A new large predatory archosaur
# from the Middle Jurassic (Bathonian) of Madagascar

**Abstract** – Here we report on the finding of new vertebrate remains from the Middle Jurassic (Bathonian) of the Mahajanga basin, NW Madagascar, that represent one of the largest predatory archosaurs from Gondwana. The remains consist of a fragmentary right maxilla bearing three teeth and seven isolated teeth that clearly belong to a single taxon. Although the scarcity of the remains renders establishment of affinities difficult, the presence of a unique combination of features including a well developed medial shelf of the maxilla, rostral and lateral teeth respectively U-shaped and sub-oval in cross-section, and very large tooth denticles (1 per mm), allows us to erect a new taxon, *Razanandrongobe sakalavae*. Additionally, the structure of the teeth, the peculiar wear of their enamel, and the morphology of the maxilla strongly suggest that *Razanandrongobe sakalavae* often crushed the bones of its prey.

**Key words**: Archosauria, teeth, maxilla, Middle Jurassic, Madagascar.

**Riassunto** – Un nuovo grande arcosauro predatore nel Giurassico medio (Bathoniano) del Madagascar.
E' qui segnalato il ritrovamento di nuovi resti di vertebrati, provenienti dal Giurassico medio (Bathoniano) del bacino di Mahajanga, Madagascar nord-occidentale, che appartengono a uno dei più grandi arcosauri predatori che abitarono le terre di Gondwana. I resti consistono in un frammento di mascella con ancora impiantati tre denti, più sette denti isolati, che appartengono chiaramente ad un solo taxon. Sebbene la frammentarietà dei reperti renda difficile stabilirne le relazioni, la peculiare combinazione di caratteri, tra cui una mensola palatale del mascellare ben sviluppata, denti rostrali e laterali rispettivamente a forma di U e sub-ovali in sezione trasversa, e carene con denticoli decisamente grandi (1 pcr mm) ci consente di erigere un nuovo taxon, *Razanandrongobe sakalavae*. La struttura dei denti, il particolare grado di usura del loro smalto e la morfologia del mascellare suggeriscono inoltre che *Razanandrongobe sakalavae* fosse solito triturare le ossa delle prede.

**Parole chiave**: Archosauria, denti, mascella, Giurassico medio, Madagascar.

\*Museo Civico di Storia Naturale, Corso Venezia 55, 20121 Milano, Italy,
e-mail: simonemaganuco@iol.it
\*\*Museo Civico di Storia Naturale, Corso Venezia 55, 20121 Milano, Italy,
e-mail: cdalsasso@yahoo.com (corresponding author).
\*\*\*Museo Civico dei Fossili di Besano, Via Prestini 5, 21050 Besano (Varese), Italy,
e-mail: museodibesano@tiscali.it

## Introduction

The Mahajanga Basin (Fig. 1) comprises a large region of north-western Madagascar, where deposition of continental, deltaic and partly marine sediments occurred since Permian times (Fig. 2A). In recent years, the Mahajanga Basin has become famous in the palaeontological literature for its Late Cretaceous (Maastricthian) invertebrates and vertebrate-rich outcrops (Maevarano and Berivotra Formations). The equally fossiliferous Late Triassic and Jurassic deposits (Isalo 'Group'), exposed over a several-hundred-kilometre-long arc along the eastern and southern margins of the basin, have been object of few research subsequent to work by Lydekker (1894) (e.g., Thevenin, 1907; Besairie, 1936; Lavocat, 1955; Bonaparte, 1986), only in the last decade have they received more attention (Flynn et al., 1997, 1999; Dal Sasso & Pasini, 2003; Maganuco et al., 2005; Buffetaut, 2005). The Middle Jurassic deposits of the Mahajanga Basin contain a peculiar and poorly known fossil vertebrate fauna. Teeth of thalattosuchian crocodyliforms, plesiosaurs and possibly ichthyosaurs, as well as dinosaurian remains (mainly sauropods), were reported in the last century (Thevenin, 1907; Besairie, 1936, 1972; Lavocat, 1955; Ogier, 1975; Bonaparte, 1986). Remains of an early tribosphenic mammal (Flynn et al., 1999a), pterosaur teeth (Dal Sasso & Pasini, 2003), sauropod teeth and one dentary (Buffetaut, 2005), and diverse theropod teeth and vertebrae have been also reported (Flynn et al., 1997; Maganuco et al., 2005).
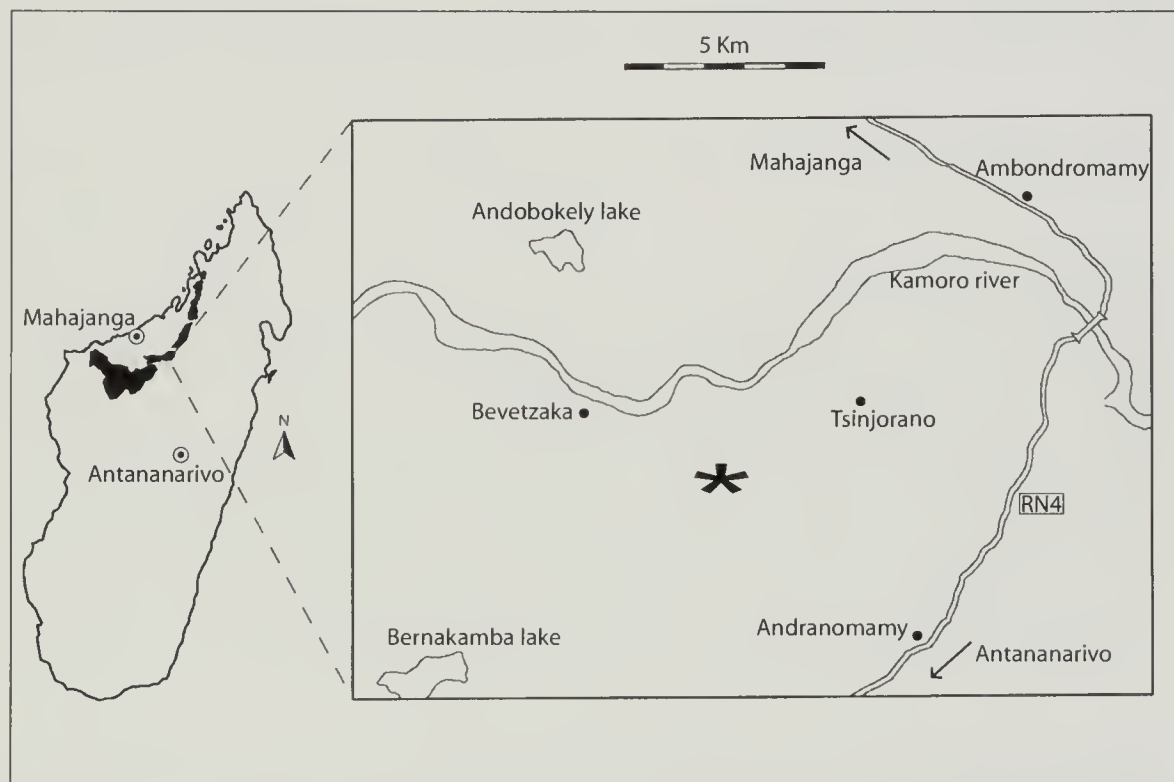


Fig. 1 - Map of the Triassic and Jurassic outcrops of the Mahajanga Basin (black areas on the left) and close-up of the localities recently prospected by the authors. Part of the material here described (the isolated teeth) comes from the area marked by the asterisk.
Fig. 1 - Mappa dei giacimenti triassici e giurassici del Bacino di Mahajanga (aree annerite nella cartina a sinistra) e particolare delle località recentemente prospettate dagli autori. Parte del materiale qui descritto (i denti isolati) proviene dall'area indicata dall'asterisco.

In October 2001, within an agreement between the Museo di Storia Naturale di Milano and the Ministère de l'Energie et des Mines together with the Direction des Mines et de la Géologie de Madagascar, some inspection by one of the authors (G. Pasini) verified the presence and the extension of fossiliferous outcrops of the Isalo IIIb Subunit (Fig. 2B), and their potential for further research as well. Under that aim, four temporary concessions to prospection (Bureau du Cadastre Minier n.3402-3405/Carte 41) were acquired in the area between Ambondromamy and Ambalanjanakomby. In April 2003, a joint expedition of the Museo di Storia Naturale di Milano and the Museo Civico dei Fossili di Besano, promoted by an Italian private sponsor (BIOE s.r.l.), gave the authors the opportunity to re-prospect the same area and to collect the first Malagasy remains of pterosaurs (Dal Sasso & Pasini, 2003), as well as the isolated teeth here examined. During the 2001 field
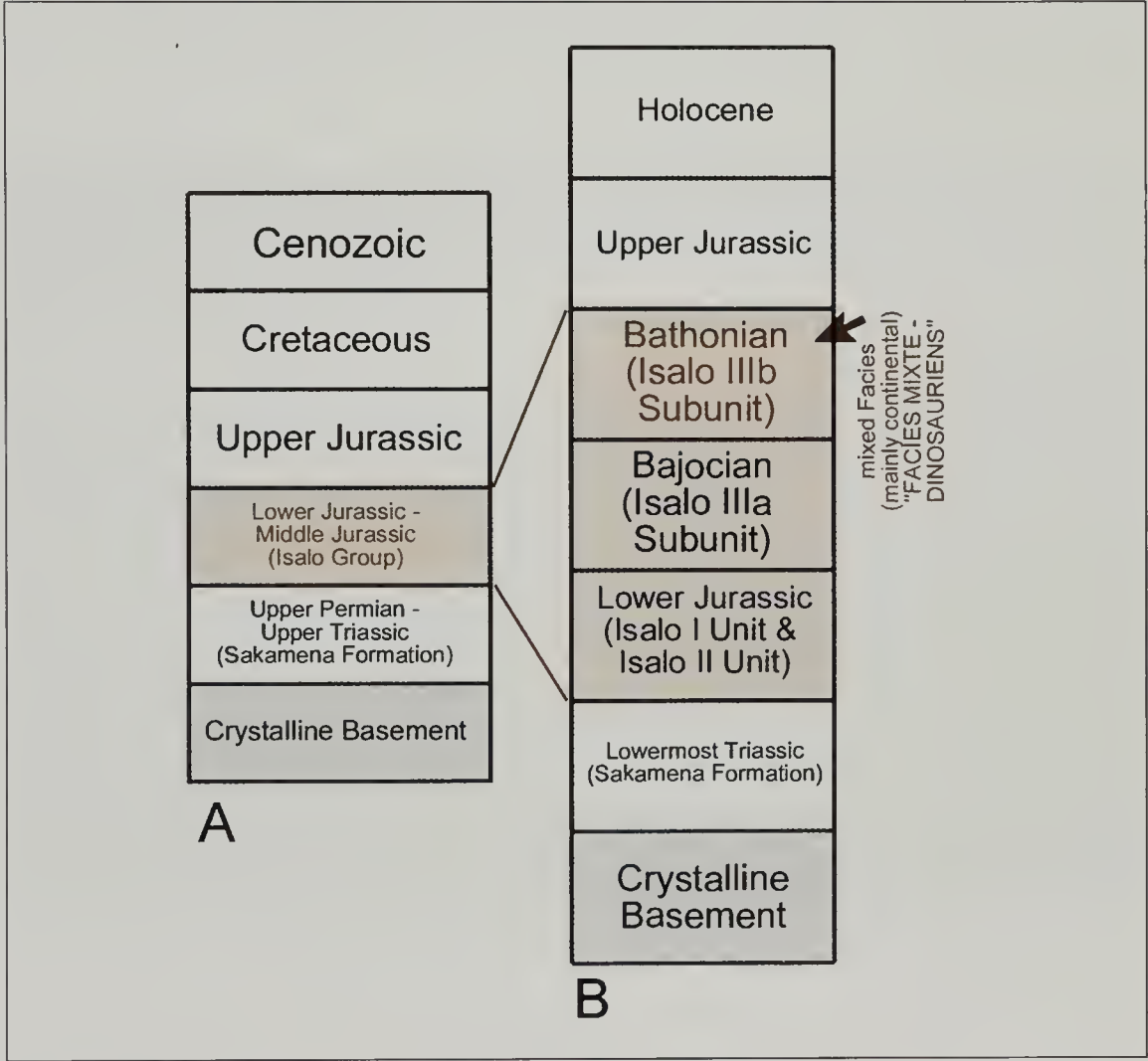


Fig. 2 - Schematic geological sections of the whole Mahajanga basin (A) and near the village of Ambondromamy (B). The arrow indicates the Isalo IIIb Subunit "Faciés mixte - dinosauriens" Bathonian *sensu* Besairie (1972), which our specimens come from. Modified from Besairie (1972).
Fig. 2 - Sezione geologica schematica generale del bacino di Mahajanga (A) e in particolare nei pressi di Ambondromamy (B). La freccia indica la Subunità Isalo IIIb "Faciés mixte - dinosauriens" Bathonian *sensu* Besairie (1972), dalla quale provengono gli esemplari. Tratta da Besairie (1972), semplificata.

survey, local collectors reported the fortuitous finding on the surface, in the neigh-
bourhood of the village of Ambondromamy (Fig. 3), of two cranial fragments with
well preserved teeth still in place, belonging to two different kinds of fossil rep-
tiles. After several events, the two cranial fragments were acquired in Europe by
Gilles Emringer and Francois Escuillié of the *Eldonia* society of Gannat, France,
with the purpose to make them available for scientific description. The first spec-
imen, a sauropod mandibular fragment now housed in the Toulouse Natural
History Museum, was studied by E. Buffetaut (Buffetaut, 2005). G. Pasini was able
to see the second specimen in June 2003 and to recognize that the teeth still
implanted in the bone were identical to the teeth he had collected in the field in the
meantime, during the prospecting activity in April 2003. Therefore the Museo
Civico di Storia Naturale di Milano acquired the specimen, in order to study it
together with the isolated teeth collected around the same area. Here we describe
all those remains as diagnostic of a new taxon, *Razanandrongobe sakalavae*, which
potentially represents the largest predator of the Malagasy Middle Jurassic terres-
trial ecosystem.



Fig. 3 - One of the outcrops of the Middle Jurassic (Bathonian) Isalo IIIb subunit near the village of
Ambondromamy.
Fig. 3 - Uno degli affioramenti della subunità stratigrafica Isalo IIIb, riferibile al Giurassico medio
(Bathoniano), nei pressi del villaggio di Ambondromamy.

## Geological setting

Between the villages of Ambondromamy and Ambalanjanakomby, about 170 km
E-SE of Mahajanga, the national road to Tananarive (RN4) crosses a succession of
badlands, locally known as *tanety* (hills), created by weathering into the Jurassic sed-

iments that constitute the eastern margin of the Mahajanga Basin (Fig. 1). These out-crops were correlated to the upper levels of the Isalo 'Group' (W Madagascar) and named 'Isalo III-Facies Continental' by Besairie (1936). Subsequently, the same author (Besairie 1972) distinguished the top of the series as 'Isalo IIIb-Bathonien Facies Mixte Dinosauriens' because of its heterolithic nature, which was verified by Boast & Nairn (1982). According to Besairie (1972) this subunit is about 190 m thick and consists of alternating, variegated sandstones and siltstones arranged in cross-bedding layers, calcareous paves and multicoloured claystone banks. Silicified wood is sometimes present. Besairie (1972) estimated a Bathonian age for Isalo IIIb (ICS stage Bathonian 167.7 – 164.7 Ma in Gradstein *et al.* [2004]) on the basis of its rich invertebrate fauna including the index echinoids *Nucleolites amplus* and *Acrosalenia colcanapi*. The isolated teeth were collected in loose sediments on the surface in the Isalo IIIb subunit composing the *tanety* located about 8 km W-NW of the village of Andranomamy, at an altitude of ~60 m (Fig. 3). During the preparation of the maxil-la we collected the matrix to analyze the sediment. The matrix is composed of a fine-grained, well sorted sandstone, with very fine-grained carbonatic cement. Quartz is the main clastic component; among the accessories, garnet and zircon are scarce and are present with about the same ratio, whereas ilmenite is more abundant, as usually seen in the alluvial deposits. Granulometry ranges from 0.2 to 0.3 mm. Silty, black-ish fragments, rich in organic matter, are also present (Pezzotta, pers. com. 2005). The latter might be related to long exposure of the specimens on the ground surface. In fact, some teeth underwent the action of the so-called "feu de brousse" (among the locals, to set fire to the grass is a common way to renovate their cultivation land). In summary, the sedimentologic parameters indicate a fluvial-lacustrine, non-marine depositional environment.

Our analysis is consistent with those reported by Besairie (1972) on the sections he made along the rim of the Mahajanga basin; in particular, there are affinities with the section called "Coupe-Route de Majunga", which is referred as continen-tal Bathonian with mixed facies, and named "Isalo IIIb-Bathonien-Facies mixte dinosauriens". Some discrepancy of data occurs in the granulometry of the sedi-ment (0.15 mm in Besairie, 1972) and in the garnet-zircon ratio, with the latter scarcer than the former, according to the same author. However, the high variabil-ity of that facies must be taken into account because of its genesis, which is testi-fied also by local heteropy. In the end, it is worth mention that the sample here ana-lyzed comes from the sediment that was in direct contact with the bone. As already noted by Lavocat (1955), there is evident difference in composition between the homogeneous, more sandy and softer beds, and the silt encasing the fossils. The encrusting nature of the silt raises the hypothesis of a pseudo-nodulisation of the fossils, linked to a peculiar diagenesis of the carcasses, in a peculiar environment of decomposition of the organic remains.

## Material and methods

The material here described is housed in the Collection of Fossil Vertebrates of the Museo Civico di Storia Naturale di Milano (MSNM V). The teeth, found isolat-ed in loose sediments, are pictured in digital photographs (Nikon Coolpix 995, 3.34

Megapixel) which were taken on them as they were collected in the field. As mentioned above, some preparation was done on the maxilla, in order to bring to light the teeth and their denticles, which in the end revealed the presence of a third erupting tooth. Measurements were taken with a digital calliper; cross-sections of the teeth were obtained by casting them with silicon RTV rubber and cutting of their epoxy-resin replicas. The cross-section drawings were made under camera lucida. In describing the teeth we utilized the following terms: TCH = tooth crown height; FABL = fore-aft basal length; BW = basal width; BCR (FABL/BW) = basal compression ratio; ER (FABL/TCH) = elongation ratio (all these terms are from Currie *et al.* [1990], and Farlow *et al.* [1991]); DSDI = denticle size difference index (Rauhut & Werner, 1995). Denticle count, where possible, was taken at mid-crown height because, as explained in the description, the size of the denticles decreases at the apical and basal ends of both carinae. The systematic terms are taken mainly from Brochu (2001). Additional systematic terms concerning the relationships among theropods, basal Crurotarsi and mesoeucrocodylians are taken respectively from Weishampel *et al.* (2004), Parrish (1993) and Sereno *et al.* (2001).

**Institutional abbreviations**

**MNHN**, Muséum national d'Histoire naturelle, Paris (France); **MOR**, Museum of the Rockies, Bozeman (Montana, USA); **MSNM**, Museo Civico di Storia Naturale, Milano (Italy); **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller (Alberta, Canada).

**Anatomical abbreviations**

**antfe/al/aj**, antorbital fenestra/articular surface for lacrimal/articular surface for jugal; **apal/aect**, articular surface for palatine/articular surface for ectopterygoid; **ic/sof**, internal choana/suborbital fenestra; **a2**, 2$^{nd}$ alveolus; **a4**, 4$^{th}$ alveolus; **antfe**, antorbital fenestra; **df**, dental foramina; **ect**, ectopterygoid; **ic**, internal choana; **ip**, interdental plates; **j**, jugal; **l**, lacrimal; **m**, maxilla; **mfe**, maxillary fenestra; **mms**, maxillary medial shelf; **n**, nasal; **pal**, palatine; **pt**, pterygoid; **rt**, replacement teeth; **s**, sulcus; **sof**, suborbital fenestra; **v**, vomer.

## Systematic Paleontology

Archosauromorpha Huene, 1946
Archosauriformes Gauthier, Kluge & Rowe, 1988
Archosauria Cope, 1869 *sensu* Gauthier, 1986
*Razanandrongobe sakalavae*, gen. et sp. nov.

**Holotype:** MSNM V5770 Fragmentary right maxilla bearing three unerupted teeth.
**Referred material:** MSNM V5771-5777, isolated teeth.
**Age and stratigraphic horizon:** Middle Jurassic (Bathonian), 167.7-164.7 MA, Mahajanga Basin, Isalo IIIb subunit, 'Facies Mixte Dinosauriens'.

**Locality:** maxilla: undetermined Hills W of Ambondromamy – teeth: hills N-NW of Andranomamy (Mahajanga Province), NW Madagascar.

**Etymology:** *Razanandrongobe*, Malagasy composite name for 'ancestor' (Razana-) of the 'large' (-be) 'lizard' (-androngo-); *sakalavae*, latin for 'of Sakalava', the ethnic group that inhabits the Mahajanga region.

**Diagnosis:** large predatory archosaur with deep, robust maxilla bearing a prominent maxillary medial shelf; thecodont tooth implantation; alveolar channels nearly straight in the sagittal plane; alveoli (as preserved) sub-rectangular in ventral view; fused interdental plates with a surface texture consisting of marked ridges and furrows extending for a short distance also above the dorsal margin of the interdental plates; heterodont dentition; incisiform rostral teeth, U-shaped in cross-section; stout lateral teeth, sub-oval in cross-section; smallest lateral teeth, globe-shaped; denticles present on both carinae in all the teeth, and very large (0.8-1.4 per mm) (unambiguous autapomorphy of the taxon).

## Description

Maxilla (specimen MSNM V5770)
The specimen consists of a maxillary fragment (Figs. 4-6), 192 mm long, 124 mm high, and 96 mm wide (as preserved) that preserves many features such as the interdental plates and a robust maxillary medial shelf. It also exposes on its lateral side five alveoli and three in situ unerupted teeth. On the basis of the curvature of the crowns and the general morphology of the bone, it should pertain to the right side of the skull. Its position in the skull and the interpretation of some features (such as the attachment areas for the palatine/ectopterygoid and for the jugal/lacrimal or the presence/absence of the antorbital fenestra) remain unclear, as these features vary according to which group the specimen is compared with. The external bony surface underwent little weathering, and is better preserved ventro-medially.

Lateral view (Fig. 4A). The preserved dorsal margin of the bone is nearly horizontal to the level of the third alveolus and then gradually slopes ventrally and forms a concave area (see dorsal view). The original ventral margin of the maxilla is preserved from the alveolus 2 to the caudal end of the bone, and seems to show that the maxilla had the same convexities in the lateral outline visible in the maxillary mid-caudal portion of several taxa. The lateral wall of the bone is totally eroded, leaving exposed the medial surface of five alveoli and three substitution teeth. According to the definitions given by Motani (1997) and Zaher & Rieppel (1999) the tooth implantation here is clearly thecodont. The dorsal end of the alveolar channels is preserved, so that we can infer that the missing lateral wall of the maxilla did not terminate far dorsally to that margin, where it would have formed the ventral margin of the antorbital fenestra or, alternatively, met the nasal. Judging from both the ER of the preserved tooth crowns (Tab. I) and the rostro-caudal diameter of the alveoli, we can also infer that the length of each alveolar channel was major than its corresponding TCH. Substitution teeth are housed in alveoli 3-5, illuminating the process of tooth replacement: replacement tooth 5 represents an early stage and was emerging in a latero-ventral direction (at about 45°) from the lateral wall of its alveolar channel; replacement
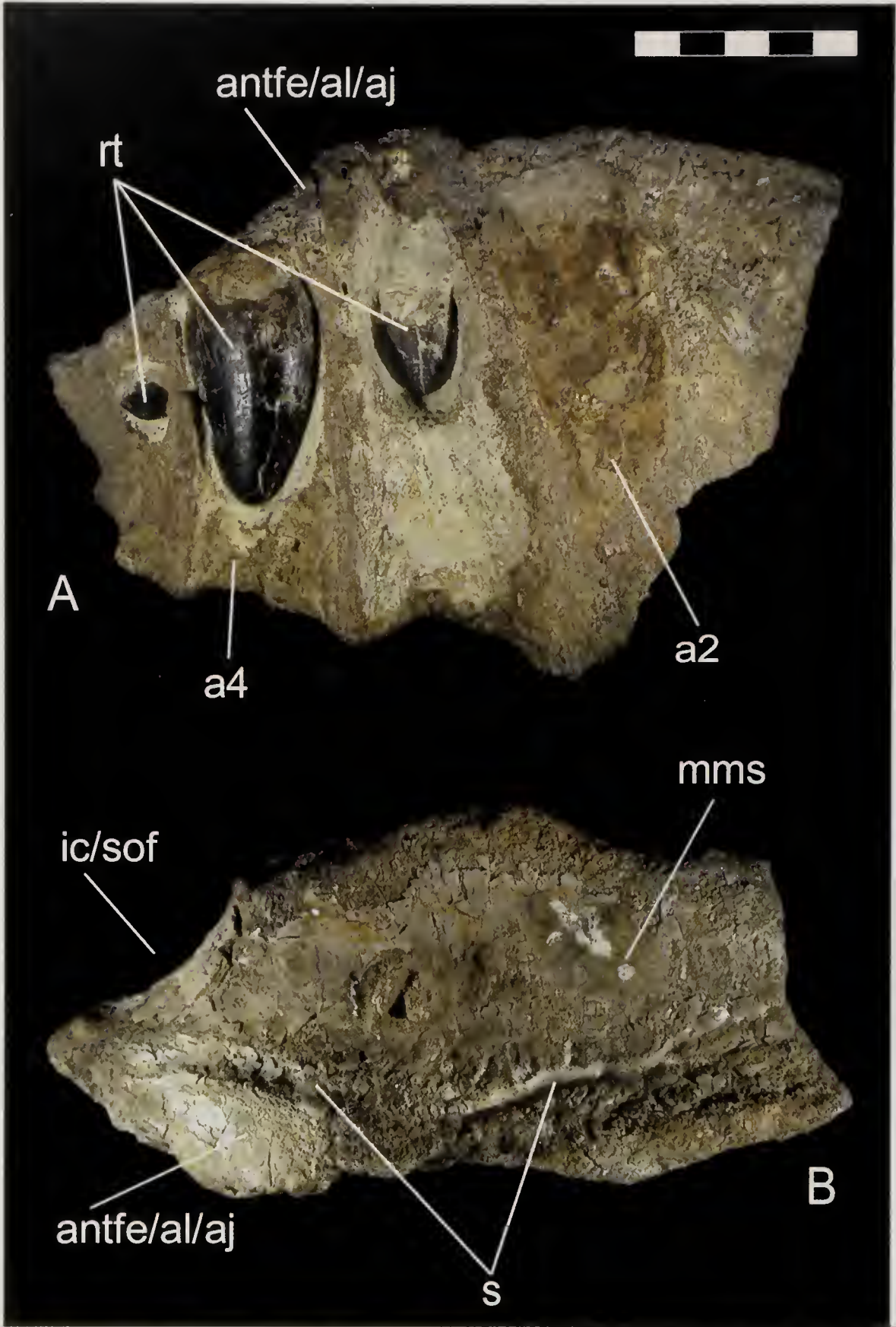
Fig. 4 - Specimen MSNM V5770 in lateral (A) and dorsal (B) views. Scale bar = 5 cm. For abbreviations see text.
Fig. 4 - Esemplare MSNM V5770 nelle viste laterale (A) e dorsale (D). Scala metrica = 5 cm. Per le abbreviazioni consultare il testo.
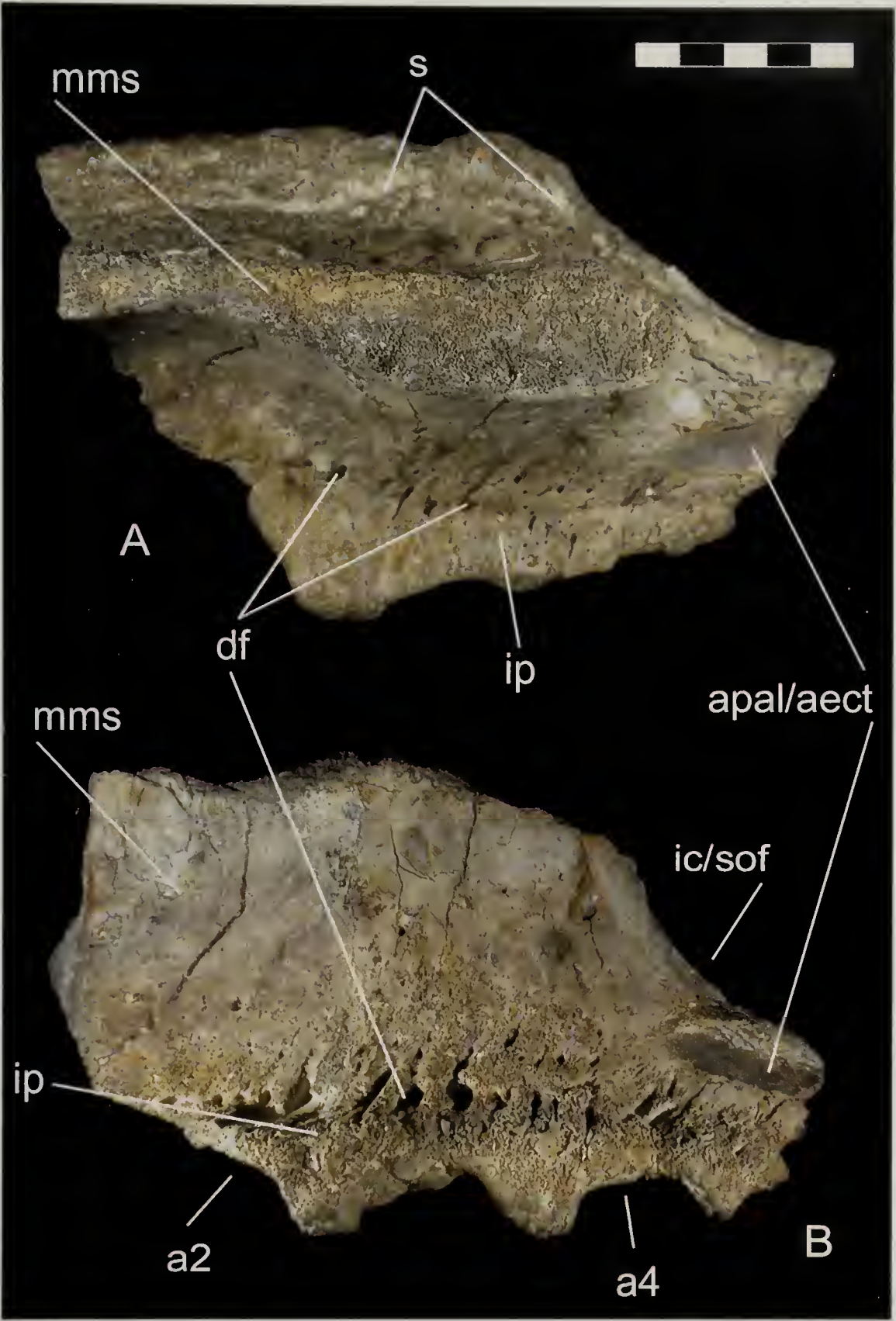
Fig. 5 - Specimen MSNM V5770 in medial (A) and ventral (B) views. Scale bar = 5 cm. For abbreviations see text.

Fig. 5 - Esemplare MSNM V5770 nelle viste mediale (A) e ventrale (B). Scala metrica = 5 cm. Per le abbreviazioni consultare il testo.

tooth 3, after having rotated to a subvertical position, was growing medial to the root of the functional tooth that occupied the alveolar channel; finally, replacement tooth 4 was growing in its alveolar channel where the resorption of the root of the functional tooth was almost complete. The tooth denticles are exceptionally large (1-1.25 per mm) and wrap around the tip of the tooth. Further characteristics of the teeth will be discussed below, in the dentition section.

Medial view (Fig. 5A).The interdental plates are fused to each other and to the ventromedial surface of the maxilla, and bear fine vertical wrinkles and marked ridges and furrows, slightly caudally inclined, that give the medial maxillary wall a rugose texture. The interdental plates taper caudally, following the curvature of the alveolar ventral margin of the maxilla. A rostro-caudally oriented row of dental foramina, that presumably served for the passage of the dental arteries, delimits the interdental plates dorsally. Within the rugose area, smaller foramina and pits are present, mostly above that row. Just dorsal to the interdental plates, the maxilla gradually becomes more inclined medially to form a stout, prominent maxillary medial shelf, which lies in a sub-horizontal plane at the level of its broken medial margin. The surface texture in this area is very much like that of the interdental plates for a height of about 15-20 mm above the row of the dental foramina, after which the maxilla is marked by an abrupt change of texture and becomes smooth. A single broad depression possibly coinciding with the positions of dentary teeth at closed jaws can be observed at the level of the second preserved alveolus. The broken medial margin of the maxillary medial shelf appears slightly sigmoid in outline, and is dorso-ventrally thicker in the mid portion of the preserved maxilla, as if it would have formed a strong median bar in that point. Adjacent to this thickened margin the ventral side of the maxillary medial shelf is stouter than in the adjacent areas, and pierced by at least 3 foramina. Rostrally, the broken medial margin of the shelf tapers to halving its dorsoventral depth. Caudally, the shelf abruptly terminates rostrally to the rostral portion of the attachment area for the palatine or ectoptery-goid. This attachment area is preserved as a well-delimited, sub-triangular depression, more marked dorsally, that lie in a vertical plane at the caudal end of the maxilla. Dorsal to the maxillary medial shelf, the maxilla is slightly inclined laterally and faintly concave, up to its lateral-most preserved dorsal margin.

Dorsal view (Fig. 4B). The most striking feature in dorsal aspect is a broad area in the caudo-lateral corner that could represent the rostro-ventral margin of the antorbital fenestra, or more simply, a concave depression on the medial side of the missing lateral wall of the bone. Another possibility is that this area represents the rostro-medial portion of the attachment area for the jugal/lacrimal. This uncertainty is due to the bad preservation of the bony surface in this point. This renders it difficult to determine if its texture indicates the attachment area of a bone or an external surface. A sulcus, presumably for the passage of a large artery (see Colbert, 1946), runs rostro-caudally 10 to 20 mm from the lateral broken edge of the maxilla for its entire length, dividing the alveolar portion of the bone from the maxillary medial shelf.

Ventral view (Fig. 5B). Judging from the preserved portions of the alveoli, they were probably subrectangular in transverse section, with their lateral alveolar margin extended farther ventrally than the medial one. Toward the caudal end of the

bone the tooth row gently arches in a lateral direction, indicating an increase in skull width. The palatal shelf, as preserved, is rather wide but its total medial extension cannot be reconstructed with accuracy. The maxilla tapers caudally forming a concave medial margin where the bone would have bordered rostrally the internal choana or the suborbital fenestra. Along this concave margin the undeformed bony wall is unbroken, continuous and naturally curved.
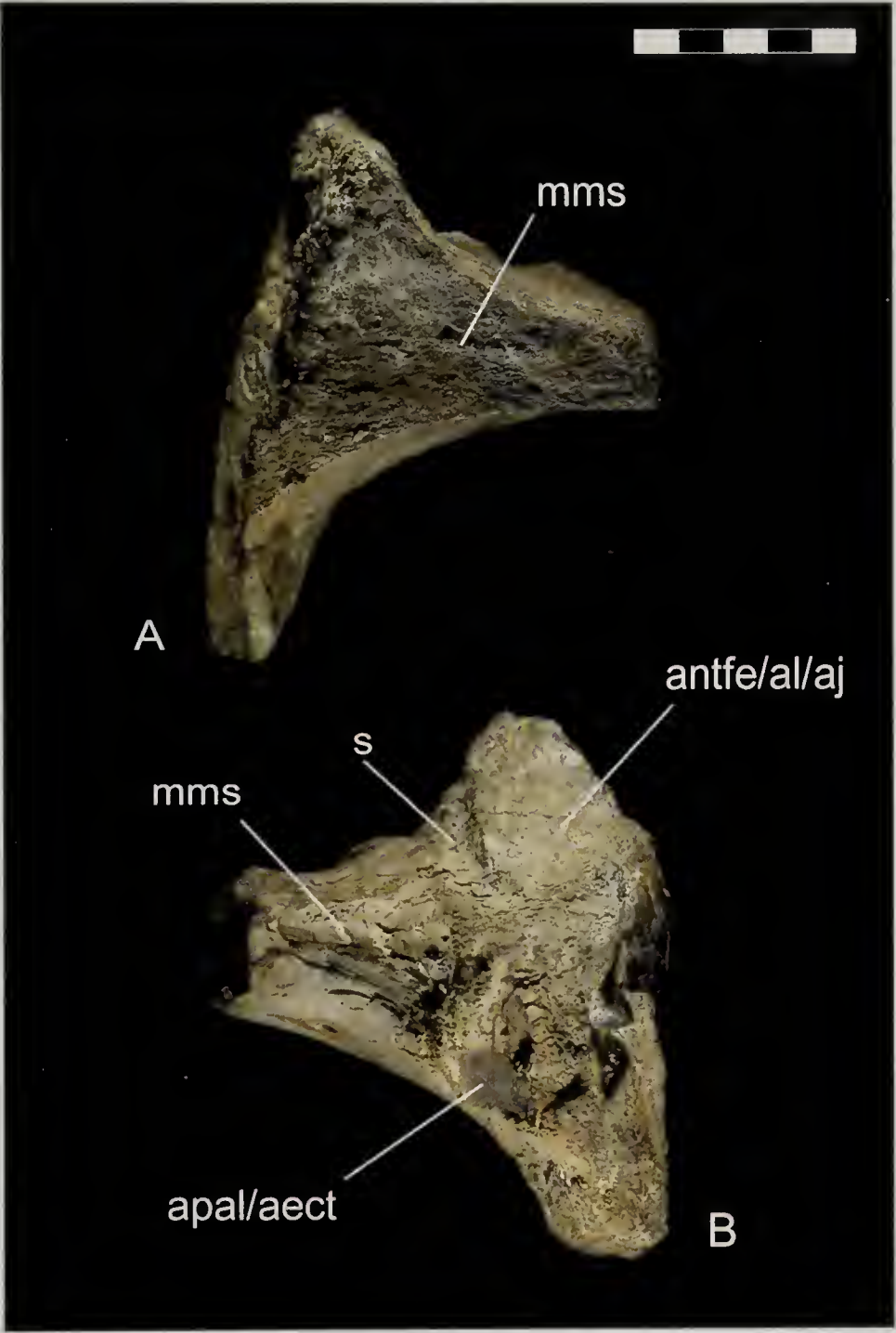


Fig. 6 - Specimen MSNM V5770 in rostral (A) and caudal (B) views. Scale bar = 5 cm. For abbreviations see text.
Fig. 6 - Esemplare MSNM V5770 nelle viste rostrale (A) e caudale (B). Scala metrica = 5 cm. Per le abbreviazioni consultare il testo.

Rostral view (Fig. 6A). In rostral view the lateral portion of MSNM V5770 appears gently convex. The alveoli match this convexity, being slightly curved medially, but their orientation can be considered definitely sub-vertical. The broken section of the maxillary medial shelf appears almost triangular, with the concave dorsal and ventral margins converging medially. The transition from the vertical portion of the maxilla bearing the interdental plates to the sub-horizontal medial-most portion of the maxillary medial shelf, which gives the medial wall a concave profile, can be seen in this view.

Caudal view (Fig. 6B). In caudal view, the wide area which is variably interpretable (see dorsal view) is visible on the dorso-lateral corner of the specimen. This area faces dorso-caudally, at an angle of about 25° from the horizontal plane. On the medial side the stouter portion of the maxillary medial shelf can be seen, and in this view its ventral wall is inclined at 45° degree and nearly straight. On the contrary, in rostral view it is regularly concave, because the shelf is less robust and the palate vault deeper. The attachment area for the palatine/ectopterygoid, present on the medio-ventral side of the bone, preserves a rim thicker dorsally. At the same level on the lateral side the ventro-laterally directed tip of the replacement tooth in the caudalmost alveolus is visible.

Dentition (specimens MSNM V5770 – V5777)

All the tooth crowns here described (Tab. I; Fig. 7) are stout, pointed, recurved, bent lingually, and bear very large denticles on both the carinae. Since no basalmost portion of the crown is intact, it is difficult to understand if there was a basal constriction between the crown and the root. All the teeth can be considered true ziphodont *sensu* Prasad & de Lapparent de Broin (2002), in having clearly individualized denticles on the carinae, which are not the result of prolongation of the enamel ridges of the crown. On the basis of the shape of the crown, we recognized three morphotypes that in all likelihood come from one taxon. The variation of the teeth is consistent with the range of variation documented for other archosaurs in which teeth vary in size, shape, and carinal orientation depending on where they occur in the jaw. It is not known whether the teeth come from the upper or the lower jaw but we can infer their position in the jaws. The first morphotype, including MSNM V5775, represents a rostral tooth. Specimens MSNM V5771-5774, 5776, and all the substitution teeth implanted into the maxilla are lateral teeth and pertain to the second morphotype. The third morphotype is represented by MSNM V5777, a small lateral tooth with a very short crown that does not appear as a scaled version of the larger lateral teeth, being rather globular. It was probably one of the caudal-most teeth. The lacking of the rostral portions of the jaws and the paucity of our sample do not allow us to understand if the smaller size of V5775 respect to most of the lateral teeth signifies that the rostral teeth were smaller than the lateral ones or if V5775 belongs to a small individual. In V5773 and V5777 only the very apical portion of the crown shows faint traces of wearing. In all other specimens the tip is markedly consumed and the wear surfaces extend on both the lingual and labial side, where the dentine is broadly exposed and preserve microscopic wear striations. Some of these striations are oriented vertically or slightly inclined caudally, but the majority of them is oriented heterogeneously. The later-

al teeth of *R. sakalavae* show their greatest wear on the lingual side (Fig. 8H), on which a U-shaped spalled surface occupies most of the apical third of the crown, whereas a long and narrower spalled surface, contacting the former apically, flattened the apical half of the twisted mesial carina. The lingual spalled surfaces cross over the tip of the crown and extend onto the labial side. The surficial enamel in



Fig. 7 - Specimens MSNM V5771-5777 in lingual (A) and distal (B) views. Scale bar = 10 cm.
Fig. 7 - Esemplari MSNM V5771-5777 nelle viste linguale (A) e distale (B). Scala metrica = 10 cm.

Tab. I - *Razanandrongobe sakalavae* n. gen. n. sp.: basic numbers and measurements of the teeth. With the exception of the specimen MSNM V5773 the tips of the crown are consumed; as a consequence, the TCHs and ERs here reported are respectively slightly lower and higher than they should be.

Tab. I - *Razanandrongobe sakalavae* n. gen. n. sp.: misure principali dei denti. Poiché, ad eccezione dell'esemplare MSNM V5773, le punte delle corone sono consumate, i valori relativi a TCH ed ER riportati sono rispettivamente leggermente più bassi e più alti che in origine.

| Specimen | Tooth crown height (TCH) in mm | Fore-aft basal length (FABL) in mm | Tooth basal width (BW) in mm | Basal compression ratio (FABL/BW) | Elongation ratio (FABL/TCH) | Number of serrations per 5 mm of mesial carina | Number of serrations per 5 mm of distal carina | Denticle size difference index (DSDI) |
|---|---|---|---|---|---|---|---|---|
| MSNM V5770* | - | - | - | - | - | - | 4 | - |
| MSNM V5770** | 46.2 | - | - | - | - | - | 5 | - |
| MSNM V5770*** | - | - | - | - | - | 4 | 4 | 1.00 |
| MSNM V5771 | 45.7 | 26.7 | 23.1 | 1.16 | 0.58 | 4 | 4 | 1.00 |
| MSNM V5772 | 33.5 | 23.1 | 18.6 | 1.24 | 0.69 | 6 | 5.5 | 1.09 |
| MSNM V5773 | 35.5 | 20.6 | 15.1 | 1.36 | 0.58 | 5 | 4.5 | 1.11 |
| MSNM V5774 | 30.3 | 18.2 | 14.2 | 1.28 | 0.60 | 5 | 5 | 1.00 |
| MSNM V5775 | 23.4 | 12.8 | 15.4 | 0.83 | 0.55 | 5 | 5 | 1.00 |
| MSNM V5776 | 20.7 | 14.5 | 12.2 | 1.19 | 0.70 | - | 6.5 | - |
| MSNM V5777 | 11.8 | 12.8 | 11.1 | 1.15 | 1.09 | 7 | 6.5 | 1.08 |

*replacement tooth in alveolus 3.

** replacement tooth in alveolus 4.

*** replacement tooth in alveolus 5.

the rostral tooth is mostly worn away on the labial side (Fig. 8I), with a U-shaped spalled surface, whereas it is still preserved lingually. In all the teeth the carinae grade into the tooth body. In the lateral teeth, both carinae are close to the midline of the crown near the tip, but not far from it they twist, with the distal carina moving slightly labially and the mesial carina moving decidedly lingually (Fig. 8G). The marked twist of the mesial carina is visible also in the erupting tooth occupying the fifth alveolus of MSNM V5770. Due to the twisting of the carinae, in cross-section at mid-height (Fig. 8A, B) the crowns of these lateral teeth appear strongly asymmetrical, with a gently arched lingual side and a strongly curved labial side that looks like the curved portion of a D. The rostral tooth V5775 differs from the others in having both carinae on the lingual side, and the labiolingual width of the tooth greater than the distance between the two carinae. As a consequence, its strongly curved labial side appears U-shaped in cross-section at mid-height the crown (Fig. 8C). A similar pattern of carinal variation occurs in the teeth of several not strictly related theropod dinosaurs (e.g., tyrannosauroids and abelisaurids) in which the carinae are strictly in a parasagittal plane in the rearmost teeth, but with a more mediolateral orientation towards the premaxilla or front of the dentary. The cross-sections at the base of all the teeth are oval to sub-circular (Fig. 8D-F). Again, the specimen V5775 differs from the others in having the axes inverted, thus resulting more expanded labio-lingually than meso-distally (Fig. 8F). The distal carina reaches the base of the crown in all the isolated teeth, whereas the mesial carina terminates at two thirds of the crown height. In all the specimens, including the rostral tooth V5775, both carinae bear denticles for all their length. The denticles are remarkably large relative to the TCH and compared with other archosauriform denticles (Farlow *et al.*, 1991; Benton, 1986; Sues *et al.*, 1996; Clark *et al.*, 2000; Gow, 2000; Campos *et al.*, 2001; Prasad & de Lapparent de Broin, 2002; Senter, 2003; Carvahlo *et al.*, 2004). Measured at mid-crown, there are 0.8-1.4 denticles per mm (Fig. 8K-N). However they vary in size along both carinae: the apicalmost denticles are slightly smaller than those immediately below, they maintain the same size up to the mid of the crown, and then gradually decrease in size toward the basal end of the carina, where they are as large as half of the denticles at mid height of the crown. In all the specimens the mesial denticles are quite eroded. However they seem as tall as the distal denticles or, in some cases, only slightly shorter. The denticles are relatively simple in form, almost as high as long, with slightly rounded tips. As one can see in mesial and distal views (Fig. 8K-N), in the denticles of *R. sakalavae* the basal width is greater than the length (between 1.6 and 1.9 times). Where preserved, the denticles of the mesial carina wrap around the tip of the tooth onto the distal carina. However this feature has limited taxonomic utility, being common in both theropod dinosaurs (Currie & Carpenter, 2000) and ziphodont crocodyliforms (Prasad & de Lapparent de Broin, 2002). The enamel forms narrow junctions between the denticles at their top, giving more continuity to the cutting edges. These junctions, together with the denticle shape, render the slits between the denticles flask-shaped in lateral view (Fig. 8K), and hourglass-shaped looking at the crown in mesial and distal views (Fig. 8N). These rounded spaces are analogous to the high pressure slots visible on the exterior surface, between the denticles in several taxa such as the basal synapsid *Dimetrodon*, the

parasuchians, and the tyrannosaurids (Abler, 2001). A fracture along the medial sagittal plane of a portion of the distal carina in the specimen MSNM V5774 exposes the interior surface of some denticles (Fig. 8J). Although the interior surface appears partly damaged, the rounded spaces are preserved on it, resembling the condition of tyrannosaurids and differing from both *Dimetrodon* and parasuchians (Abler, 2001), which lack them. Looking at the edge of both carinae the denticles appear slightly inclined toward the tip of the crown. In all the teeth of *R. sakalavae*, blood grooves extend from the base of the spaces (i.e. between the bases of adjacent denticles) onto the surface of the crown. They are macroscopically visible and, following the denticle orientation, are slightly inclined toward the base of the crown. The enamel, where preserved, is smooth and has the same texture surface in all the specimens, except for V5775 which bears vertical striations on the basal third of the lingual surface. A dense pitting, due to surface micro-damaging by sediment granulation, notched the enamel surface.

## Taxonomic affinities

Due to the fragmentary nature of our material, *Razanandrongobe sakalavae* lacks almost all the characters used in archosauromorph phylogenetic analyses (Sereno, 1991; Parrish, 1993; Juul, 1994; Benton & Walker, 2002). In spite of that, the general morphology of both maxilla and dentition allowed us to make comparison with several archosauromorph taxa and identify some features that could help to establish its affinities. In order to better understand the taxonomic significance and the evolutionary history of these features we compared our material not only to the derived archosaur groups with which it shows potential affinities, but also to non-archosaurian archosauromorphs (Fig. 10).

Among archosauromorphs, the presence of tooth denticles has been reported in several groups, including parasuchians and rauisuchians (Abler, 1997), *Ornithosuchus* (Farlow *et al.*, 1991), euparkerids (Wu & Russell, 2001; Senter, 2003), dinosaurs (Weishampel *et al.*, 2004), "sphenosuchians" (Wu & Chatterjee, 1993; Clark *et al.*, 2000), "protosuchians" (Farlow *et al.*, 1991; Sues *et al.*, 1996; Gow, 2000) and ziphodont crocodyliforms (Colbert, 1946; Langston, 1975; Willis & Mackness, 1996; Prasad *et al.*, 1999; Campos *et al.*, 2001; Carvalho *et al.*, 2004). On the contrary, they are absent in the teeth of basal archosauromorphs, such as Protorosauria (Nosotti, pers. comm. 2005) and Rhynchosauria (Carroll, 1988), and basal diapsids (Carroll, 1988). Therefore this character could represent a synapomorphy of Archosauriformes, including *R. sakalavae*. Unfortunately, with few exceptions (e.g. *Euparkeria* [Senter, 2003]) only the presence/absence of denticles has been reported in close outgroups to Archosauria. This lack of published descriptions of other denticle-related characters makes it difficult to test if denticles contain informative taxonomic characters at high systematic levels among archosauromorphs (for example, the blood grooves at the bases of the denticles are visible in both *Euparkeria* [Senter, 2003] and some theropods [Currie *et al.*, 1990; Maganuco *et al.*, 2005] but in literature we were not able to find information about their presence/absence in other taxa including ziphodont crocodylomorphs). According to Juul (1994) it is not yet clear even at which hierarchic level the occur-
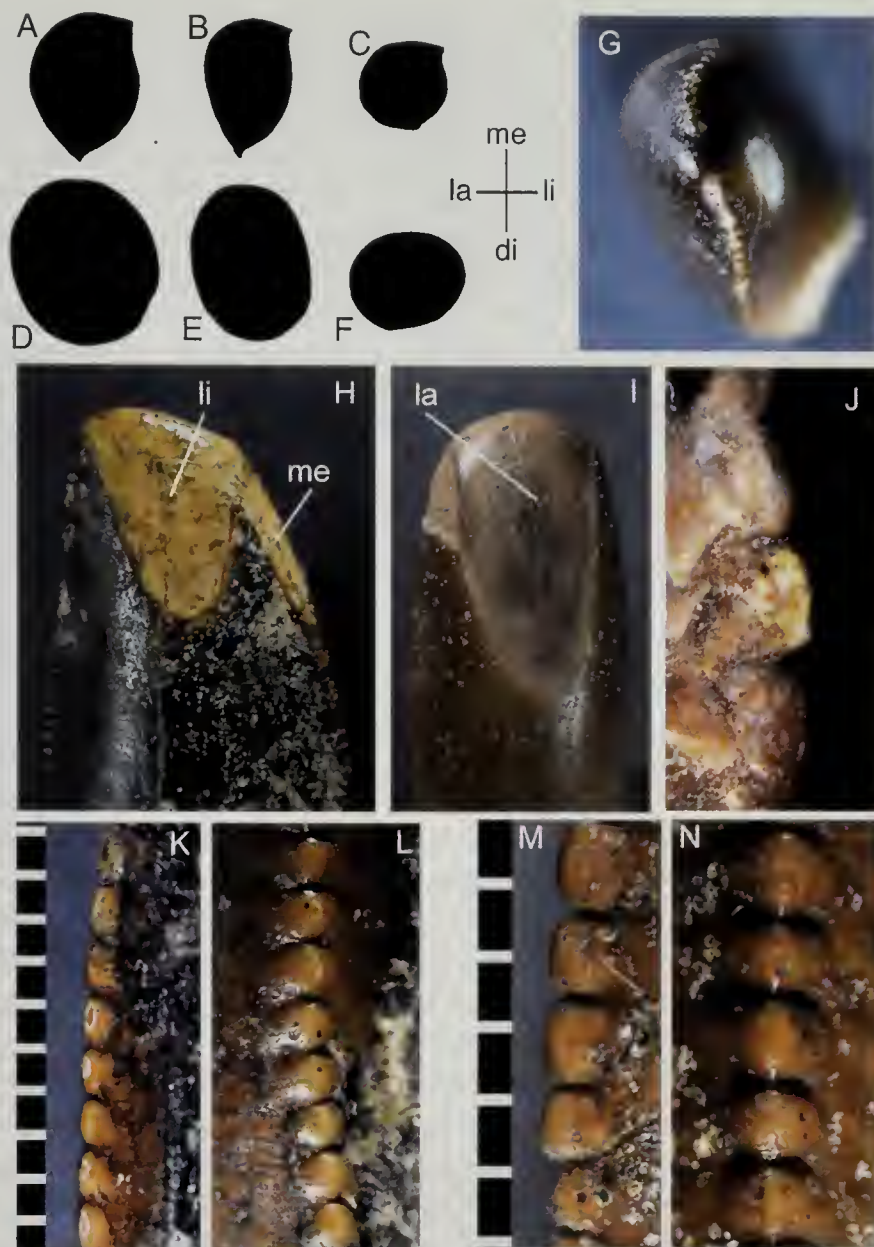
Fig. 8 – Some features of the teeth of *Razanandrongobe sakalavae* n. gen. n. sp.: specimens MSNM V5772 (A, D), V5773 (B, E), and V5775 (C, F) in cross-sections at mid-height (A-C) and at the base of the crown (D-F); specimen MSNM V5773 in apical view (G), showing the twisting of the carinae; tooth wearing visible as spalled surfaces on the lingual side of the specimen MSNM V5772 (H) and labial side of the specimen MSNM V5775 (I); interior of the denticles (J) visible thanks to a fracture along the medial sagittal plane of the distal carina in the specimen MSNM V5774; close-ups of the denticles of the specimen MSNM V5771 seen in lingual (K) and distal (L) views; close-ups of the denticles of the specimen MSNM V5773 seen in lingual (M) and distal (N) views. In A-G the directions of the axes are abbreviated as follows: di, distal; la, labial; li, lingual; me, mesial. Scale bars are in mm. Fig. 8 – Alcune caratteristiche dei denti di *Razanandrongobe sakalavae* n. gen. n. sp.: esemplari MSNM V5772 (A, D), V5773 (B, E) e V5775 (C, F) in sezione trasversa a metà altezza (A-C) e alla base della corona (D-F); vista apicale dell'esemplare MSNM V5773 (G), che mostra la torsione delle carene; grado di usura dei denti, evidenziato da piani di levigatura sul lato linguale dell'esemplare MSNM V5772 (H) e su quello labiale dell'esemplare MSNM V5775 (I); superficie interna dei denticoli (J) visibile grazie ad una frattura lungo il piano sagittale mediale della carena distale nell'esemplare MSNM V5774; particolare dei denticoli dell'esemplare MSNM V5771 in vista linguale (K) e distale (L); particolare dei denticoli dell'esemplare MSNM V5773 in vista linguale (M) e distale (N). In A-G le direzioni degli assi sono abbreviate nel seguente modo: di, distale; la, labiale; li, linguale; me, mesiale. Le scale metriche sono in mm.

rence of thecodont dentition may be considered a diagnostic feature, relative length of root to crown has not yet been quantified for many archosauromorphs, and the tooth implantation of some basal forms has been described in a confusing manner. In any case such a kind of tooth implantation clearly seems to be diagnostic for more inclusive taxa than Archosauria (Sereno, 1991), being shared without doubt by most of the Archosauriformes. Again, as pointed out by Juul (1994), on the basis of the published material available to us it was not possible to establish the exact distribution and condition of the interdental plates within Archosauromorpha. Nevertheless, they are absent in rhynchosaurs and *Prolacerta* (Juul, 1994); present but not fused in: *Euparkeria* (Senter, 2003), the rauisuchids (Juul, 1994), the ornithosuchid *Ornithosuchus* (Juul, 1994), the sauropodomorph *Massospondylus* (Juul, 1994), many theropods (Holtz, 2000), and the "protosuchians" (Sues *et al.*, 1996); and present and fused to each other in some theropod taxa (Holtz, 2000; Senter, 2003), MSNM V5770, the poposaurid *Teratosaurus* (Galton, 1985), mesoeucrocodylians (pers. obs. 2004-2005), and, at least judging from photos, also in other Crocodyliformes. So the condition "interdentental plates present but unfused" could represent at the same time a synapomorphy of Archosauriformes, and the plesiomorphic condition for Theropoda (in which they became fused independently in different groups), poposaurids, and Crocodyliformes (among whom fused interdental plates developed once). So, the dentition and the tooth implantation suggest that *R. sakalavae* belongs to Archosauriformes, and its condition of the interdental plates places it within Archosauria. Looking at the general morphology of both maxilla and dentition, *R. sakalavae* does not show any significant resemblance either with basal Archosauromorpha such as the Protorosauria or the highly specialized Rhynchosauria (Carroll, 1988), or basal Archosauriformes such as the Proterosuchidae (Carroll, 1988), Erythrosuchidae (Gower & Sennikov, 2000), Proterochampsidae (Nash, 1975), and Euparkeridae (Wu & Russell, 2001; Senter, 2003), basal ornithodirans such as *Scleromochlus* (Benton, 1999), and the crurotarsian ornithosuchids (Carroll, 1988; Sereno, 1991) and *Erpetosuchus* (Benton & Walker, 2002). All these forms can be easily dismissed, because they have homodont dentition, TCH major than maxillary depth, maxilla relatively low in profile, and do not have maxillary medial shelves and fused interdental plates (but for the distribution of the interdental plates see above). The heavily built skull and dentition of *R. sakalavae* do not show any resemblance with Pterosauria, so the latter can be dismissed too without taking care of its controversial affinities (Brochu, 2001). Also the herbivorous aetosaurs and the long snouted parasuchians (Carroll, 1988; Sereno, 1991), belonging to the Crurotarsi, can be excluded, because of their highly specialized skulls. The basalmost crurotarsian showing some affinities with *R. sakalavae* are the Prestosuchidae (Parrish, 1993). In lateral view, the Porto Alegre specimen of *Prestosuchus* figured by Parrish (1993: 4C) superficially resembles *R. sakalavae* in maxillary depth, ratio between the TCH and depth of the maxilla, shape of the caudal portion of the maxilla and sutural surface between maxilla and jugal. In addition, also the prestosuchids attain a medium to large size, and present a certain degree of heterodonty (Parrish, 1993), with caniniform rostral teeth, and compressed and recurved caudal teeth. Moreover, in the prestosuchid *Saurosuchus galilei* (Alcober, 2000) the rostralmost medial portions of the maxillae form two

medial shelves meeting medially and forming a short secondary palate. Also the poposaurid *Teratosaurus* superficially resembles *R. sakalavae* in lateral view, but following Parrish (1993) we can conclude that the resemblance in skull profile among the large headed carnivorous taxa such as Prestosuchidae, Rauisuchidae, Poposauridae, some theropods and Erythrosuchidae is probably the result of their adaptation to the same ecological role as medium-sized to large terrestrial carnivores. Summing up, thanks to its features *Razanandrongobe sakalavae* can be reasonably placed within the Archosauria but not among the basal members of this taxon. Therefore it must be compared with more derived predatory archosaurs, i.e. theropods and crocodylomorphs. This is consistent with the fossil record of Archosauria - Crocodylomorpha and Theropoda are the only carnivorous archosaurian lineages known to have survived the Triassic (Sereno, 1991; Parrish, 1993; Brochu, 2001). The possible affinities of *R. sakalavae* with theropods and crocodylomorphs are discussed in the following sections.

Theropod affinities

In comparing *Razanandrongobe sakalavae* with Theropoda (Fig. 9A, D), the attachment area located on the medial side of the maxilla must be considered the attachment for the palatine; the recess just caudal to the maxillary medial shelf must be considered the rostro-lateral corner of the internal choana; and the concave area on the lateral side of the specimen could alternatively represent the attachment for the jugal, the rostral portion of the antorbital fenestra, or a depression on the medial side of the missing lateral wall of the bone. Turning the identification around, among theropods (Rauhut, 2003; Weishampel *et al.*, 2004) we can easily dismiss the following groups (or at least their currently known members) because they do not show any of the hallmarks of *R. sakalavae*: Coelophysoidea, Ceratosauridae, Noasauridae, Allosauroidea (including Allosauridae, Sinraptoridae, and Carcharodontosauridae), Compsognathidae, Ornithomimosauria, Oviraptorosauria, Therizinosauridae, Alvarezsauridae, Troodontidae, Dromaeosauridae, and Avialae. It is worth mentioning, however, that among predatory dinosaurs only the small-bodied troodontids have teeth with denticles as large as - or even larger than - *R. sakalavae* relative to TCH (Currie *et al.*, 1990; Farlow *et al.*, 1991). Eventually, we did not find any resemblance in size and shape between the teeth of *R. sakalavae* and the isolated teeth from the same Middle Jurassic strata recently referred to Theropoda incertae sedis (Maganuco *et al.*, 2005). *Razanandrongobe sakalavae* shows some hallmarks of the Cretaceous Abelisauridae (Sereno *et al.*, 2004), such as subrectangular alveoli, fused interdental plates heavily textured and rugose, relatively low-crowned teeth (except for *Carnotaurus*, which has elongate and slender crowns), and, possibly, broad maxillary-jugal contact. However, the corresponding portion of the maxilla in the abelisaurids (Sampson, 1998), roughly comprised between the alveoli 7-11 in a whole series of about 15-16, has not a well-developed maxillary medial shelf, and bears a row of dental foramina that are larger, and more regular in shape than those of *R. sakalavae*, and are placed in a tidy row just above the interdental plates. The teeth of *R. sakalavae* do not show the typical features of the abelisaurid teeth, such as: lateral crowns drop-shaped in cross-section (Candeiro *et al.*, 2004) and decidedly more flattened labio-lingually than those of *R. sakalavae*; rostral teeth D-shaped,
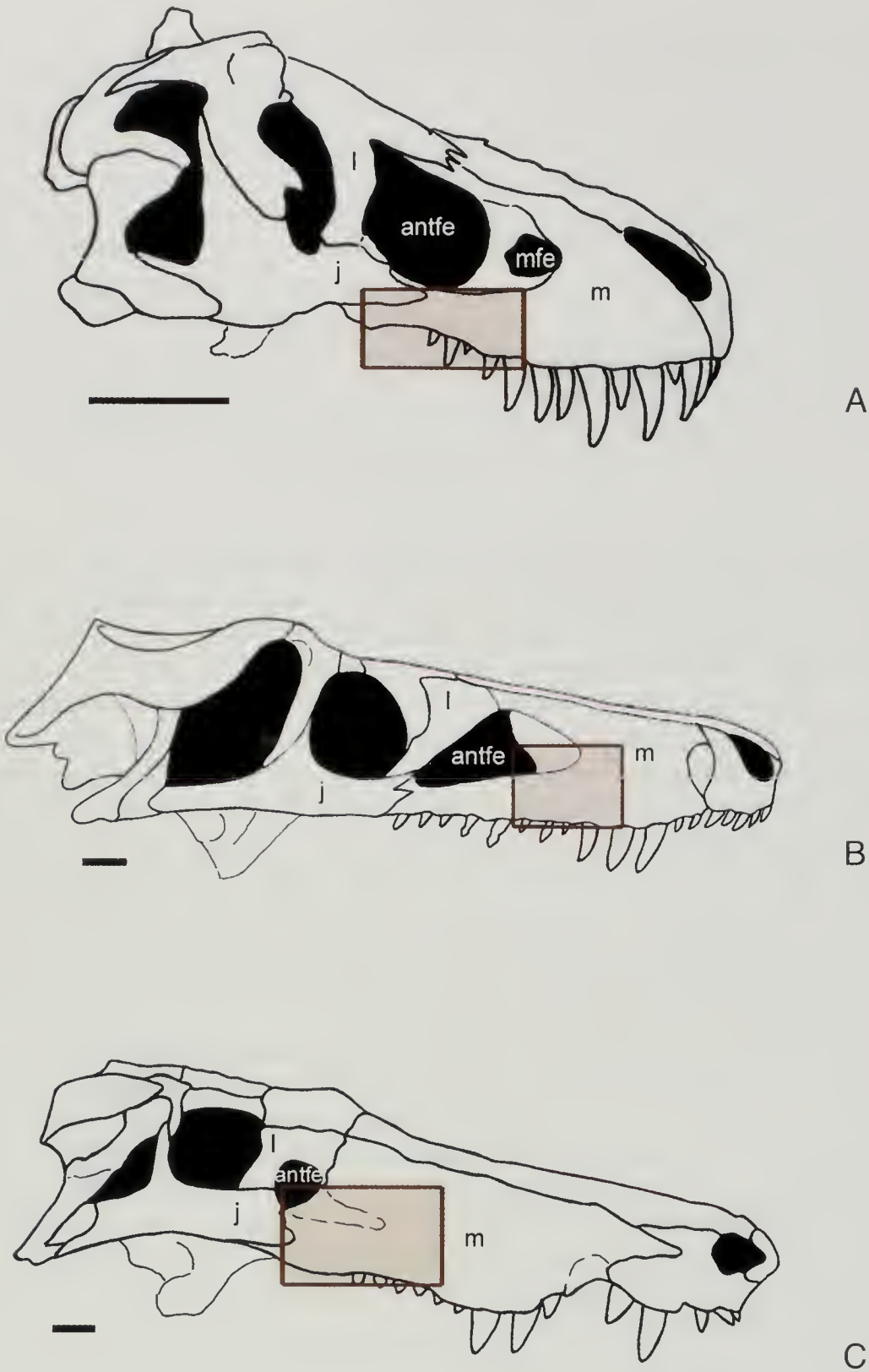
Fig. 9 – Lateral and palatal views of the skulls of: A and D, the theropod *Tyrannosaurus* (redrawn from Carr [1999]); B and E, the "sphenosuchian" *Dibothrosuchus* (redrawn from Wu & Chatterjee [1993]); and C and F, a generalized peirosaurid based on both *Uberabasuchus* (Carvalho *et al.*, 2004) and *Lomasuchus* (Gasparini *et al.*, 1991). Scale bar equals 25 cm in A and D, and 1 cm in B, C, E, and F. The coloured rectangle approximately indicates the portion of the skull corresponding to the specimen MSNM V5770. For abbreviations see text.
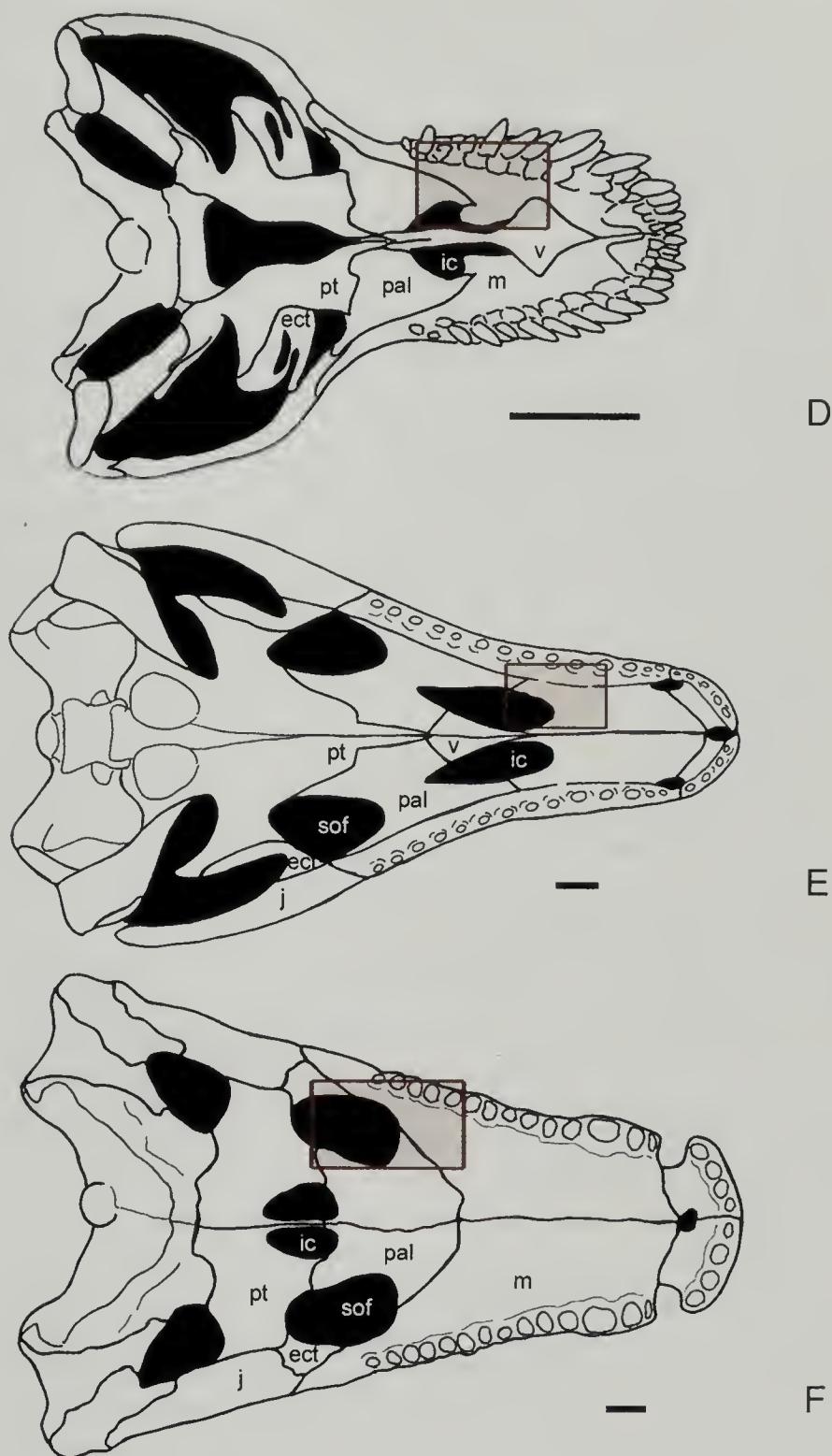
Fig. 9 – Viste laterale e palatale dei seguenti crani: A e D, il teropode *Tyrannosaurus* (ridisegnato a partire da Carr [1999]); B ed E, lo "sfenosuco" *Dibothrosuchus* (ridisegnato a partire da Wu & Chatterjee [1993]); C ed F, un peirosauride generalizzato basato sui due generi *Uberabasuchus* (Carvalho *et al.*, 2004) e *Lomasuchus* (Gasparini *et al.*, 1991). La scala metrica è di 25 cm in A e D, e di 1 cm in B, C, E ed F. Il rettangolo colorato indica approssimativamente la porzione del cranio corrispondente all'esemplare MSNM V5770. Per le abbreviazioni consultare il testo.

i.e. with a labio-lingual axis considerably shorter than that of *R. sakalavae*; blood grooves markedly inclined toward the base of the crown (Kellner & Campos, 2002; pers. obs. 2004); in the abelisaurids the areas of the crown adjacent to the carinae are flat or concave whereas the denticles of *R. sakalavae* grade into the tooth body; the abelisaurid denticles are pointed and decidedly smaller than those of *R. sakalavae* (pers. obs. on abelisaurid teeth housed in MSNM; Kellner & Campos, 2002). The rostral tooth of *Razanandrongobe sakalavae* resembles the premaxillary teeth of Tyrannosauroidea in being incisiform and U-shaped in cross-section. The sides of the rostral tooth of *R. sakalavae* are not flattened as in Tyrannosauridae, looking more like the premaxillary teeth of *Stokesosaurus* (Holtz, pers. comm. 2004), *Eotyrannus* (Hutt *et al.*, 2001), or the Jurassic teeth described by Zinke (1998) and referred to the basal tyrannosauroid *Aviatyrannis* by Rauhut (2003), but not the tooth referred to *Aublysodon* (Lehman & Carpenter, 1990: fig. 4) that lacks denticles on the carinae. On the other hand, contrary to the basal Tyrannosauroidea (Holtz, 2001b; Hutt *et al.*, 2001) *R. sakalavae* possesses lateral teeth incrassated as in – or even more than - the Cretaceous Tyrannosauridae (cross-section greater than 60% wide mediolaterally as long rostrocaudally is a tyrannosaurid synapomorphy [Holtz, 2001a]). Despite of the relatively great size of the denticles in Tyrannosauroidea (Farlow *et al.*, 1991; pers. obs. 2004 on MOR and TMP material), the denticles of *R. sakalavae* (0.8-1.4 per mm) are larger than those borne in tyrannosaurid teeth with comparable TCH. In most of our specimens, the denticles are even larger than those preserved in the largest teeth of *Tyrannosaurus* (1.2 per mm [Farlow *et al.*, 1991]). The presence of round, voided strengthening structures between the denticles have not yet been studied in a sufficient number of taxa to test their systematic significance. In *R. sakalavae* the denticles are simpler in form and do not possess the thin groove that in tyrannosaurid teeth runs along the apices of the denticles (Abler, 1997). Lastly, the blood grooves in *R. sakalavae* resemble those of the tyrannosaurids in having a similar degree of orientation toward the base of the crown (Currie *et al.*, 1990), but differ from those of basal tyrannosauroids, in which they are perpendicular to the edge of the crown (Zinke, 1998). If related to the Tyrannosauroidea, MSNM V5770 would represent the caudal end of a tyrannosaurid right maxilla, being in contact with the jugal dorso-caudally, with the palatine ventrally, being located just below the antorbital fenestra, and bordering rostro-laterally the internal choana. The alveoli of *R. sakalavae*, as preserved, appear slightly less rounded than in the tyrannosauroids (pers. obs. 2004 on MNHN, MOR and TMP tyrannosaurid material; Hutt *et al.*, 2001). Although in tyrannosaurids the maxillary medial shelf is well-developed and placed well dorsal to the level of the tooth row, the maxillary medial shelf of MSNM V5770, at scale, is too massive and too extended medially (Brochu, 2003; Carr, pers. comm. 2004; pers. obs. 2004). Moreover, the angle formed by the maxillary medial shelf with the main body of the maxilla in Tyrannosauridae ranges from 125° to 140° (pers. obs. 2004 on MNHN, MOR, MSNM and TMP tyrannosaurid material), whereas in *R. sakalavae* it is 110° to 120° (Fig. 6A, B). Finally, the interdental plates are separated in Tyrannosauridae (Currie, 2003; Hurum & Sabath, 2003), although they are not clearly differentiated from the medial surface of the maxilla in some basal tyrannosauroids like *Eotyrannus* (Hutt *et al.*, 2001). The only other large-sized theropods with a developed maxillary medial shelf and labiolingually expanded teeth

are the spinosaurids. Unfortunately, basal spinosaurids from the Jurassic are not yet known, and the highly derived snouts of the known spinosaurids (Sereno *et al.*, 1998; Dal Sasso *et al.*, 2005), which all come from Cretaceous sediments, differ from *R. sakalavae* in having: palatal shelves that meet forming an acute angle (about 45°); highly modified palatal shelves in which the not well-defined interdental plates are placed lateral to the paradental lamina that covers the alveoli secondarily medially; subcircular alveoli; homodonty in tooth shape; high crowns; and carinae unserrated or with very fine serration. Very large denticles (even 1.2 per mm) are present in some teeth (Farlow *et al.*, 1991; pers. obs. 2005) referred to the Torvosauridae, a taxon known from the Middle Jurassic and usually considered to be the sister group of the Spinosauridae (Sereno *et al.*, 1998). However, the teeth of the torvosaurids are labiolingually compressed, and their maxilla (Allain, 2002; pers. obs. 2004 on MNHN material) is low and lacks a well-developed maxillary medial shelf.

Crocodylomorph affinities

Among the crocodylomorphs, "protosuchians" (Nash, 1975; Sues *et al.*, 1996; Gow, 2000), thalattosuchians (pers. obs. 2005), dyrosaurids (pers. obs. 2005), notosuchids (Buckley *et al.*, 2000; Gomani, 1997), *Libycosuchus* (Stromer, 1914), *Sphagesaurus* (Pol, 2003), *Araripesuchus* (Ortega & Gasparini, 2000), and *Sarcosuchus* (Sereno *et al.*, 2001) do not show any significant resemblance with our specimens. To throw light on the hypothetic crocodylomorph affinities of our specimen we looked at the different evolutionary stages of development of the maxillary medial shelf in the remnant crocodylomorph groups (Langston, 1973), interpreting consequently the other features visible in our specimens. An initial stage of development of the maxillary medial shelf can be seen in some basal crocodylomorphs, the "sphenosuchians" (Walker, 1972; Walker, 1990; Wu & Chatterjee, 1993; Sues *et al.*, 1996; Clark, 2000; Clark & Sues, 2002). In the "sphenosuchians" *Sphenosuchus* (Walker, 1990) and *Dibothrosuchus* (Wu & Chatterjee, 1993) (Fig. 9B, E) there is a relatively short secondary palate formed mainly by the rostral half of the maxillae that is rostral to the internal choanae. The maxillae form a consistent part of the lateral margin of the internal choanae and do not contribute to border the suborbital fenestrae, the palatines contact medially the caudal halves of the maxillae and form the caudolateral margins of the internal choanae, and the ectopterygoids do not contact the maxillae. The rostral margin of the internal choana is at the same level of the rostralmost portion of the antorbital fossa, the maxillary border gently arches laterally and is deep, deeper than the TCH. *Razanandrongobe sakalavae* is compatible with a similar disposition of the bones bordering the internal choanae. No traces of the rostromedial wall of the antorbital fossa are visible in *R. sakalavae*, but this could depend by the fact that our maxilla lacks all its lateral portion. Other than for its large size, *R. sakalavae* differs from the "sphenosuchians" in having the attachment area for the palatine reaching the level of the rostral margin of the internal choana, and the ventral margin of the maxilla tapering caudally. Taking into account these features, in accepting the sphenosuchian topology of the bones we can hypothesize that *R. sakalavae* had a more developed maxillary medial shelf, the internal choanae more retracted caudally, and a probably smaller rostral margin of the antorbital fenestra, displaced

more caudally too. In short, it should have been like an intermediate form between the basal "sphenosuchians" and the more derived mesoeucrocodylians (see below), a possibility consistent with its Bathonian age (the "sphenosuchians" lived up to the Early Jurassic, while the terrestrial mesoeucrocodylians [i.e. metasuchians] are known from the Late Jurassic [Gomani, 1997]). The "sphenosuchians" differ from *R. sakalavae* also in the dentition (Wu & Chatterjee, 1993; Sues *et al.*, 1996; Clark, 2000), which is heterodont, but the rostral teeth do not bear denticles, and the lateral teeth are labiolingually compressed, base-constricted, and bear small denticles (about 8 per mm). In mesoeucrocodylians the maxillary contribution to the secondary palate is significantly increased with respect to the "sphenosuchians". The maxillae participate in bordering the suborbital fenestrae and often contact the ectopterygoids (this would be the case in *R. sakalavae*, which could have had small suborbital fenestrae or a great participation of the ectopterygoids to the lateral margin of the suborbital fenestrae), but are nearly excluded from bordering the internal choane, which are located well behind the caudal end of the tooth row (not preserved in our specimen), back to a caudal extension of the palatines that are close to the midline of the skull. Additionally, in the mesoeucrocodylians the antorbital fenestra is greatly reduced or absent, and the caudal portion of the maxilla broadly contacts the lacrimal (this attachment area would correspond to the concavity on the dorso-caudal margin of the specimen MSNM V5770). The specimen MSNM V5770 matches the shape of the mid part of the maxilla of the Late Cretaceous Peirosauridae (Fig. 9C, F) in both lateral (Carvahlo *et al.*, 2004) and palatal (Gasparini *et al.*, 1991) views. As in *Razanandrongobe sakalavae*, in *Lomasuchus* (Gasparini *et al.*, 1991) the concavity of the maxillary medial shelf is more marked rostrally, and broad depressions at the level of the middle of the tooth row can be seen on the palate where occlusal contact occurs with the large mandibular teeth. In our specimen, the cracking along the stouter portion of the maxillary medial shelf would be close to the suture between the maxillae and rostral portion of the palatine. However, in *R. sakalavae* the maxilla and the alveolar channels are more vertical, the palate is deeper, and the "wave" in the tooth row (sensu Gasparini *et al.*, 1991) is more marked and closer to the attachment area for the lacrimal, suggesting a snout higher and shorter than that of the peirosaurids. Also the dentition is not particularly similar to that of the peirosaurids, which have rostral teeth subcircular in cross-section, and caudalmost lateral teeth globe-shaped but with a pronounced neck. Moreover, in all the known members of the Peirosauridae the denticles are fine (Carvalho *et al.*, 2004). Among the mesoeucrocodylians, the baurusuchids (Campos *et al.*, 2001) and sebecosuchids (Colbert, 1946) have deep and nearly vertical maxillae, but their similarities with *R. sakalavae* are less numerous than those the peirosaurids have. Indeed in the baurusuchids the shape of the maxilla and its relations with the surrounding bones appear hardly compatible with the shape of MSNM V5770 [Riff, pers. comm. 2005], whereas in the maxilla of the sebecosuchids, although more compatible with the topology of the bones in MSNM V5770, the alveolar border does not form "waves" and the attachment for the ectopterygoid is retracted further caudally. Some details of the maxilla of *Sebecus icaerorhinus*, figured in medial view by Colbert (1946: fig. 2), resulted however important for comparison purpose. In *Sebecus*, as well as in extant

Crocodylia (pers. obs. 2005 on skulls of *Melanosuchus niger* and *Crocodylus niloticus* in MSNM) and some other mesoeucrocodylians (pers. obs. 2004 on MNHN material), the maxillary medial shelf lies just above the level of the tooth row, whereas in *R. sakalavae* the palate is deeper. Unfortunately, we were not able to check this feature in the "sphenosuchians". *R. sakalavae* resembles extant representatives of the Crocodylia (Brochu, 1999; pers. obs. 2005) in having the attachment of the ectopterygoid that reaches the level of the tooth row, and a small suborbital fenestra. In extant crocodiles, however, the snout is definitely flattened dorso-ventrally, and the alveoli curve medially not far above the palatal shelf (Brochu, pers. comm. 2004) and do not form vertical channels as they do in MSNM V5770. Moreover, the teeth of the ziphodont Crocodylia (such as the Pristichampsinae) bear fine denticles (Prasad & de Lapparent de Broin, 2002).

Summary

*Razanandrongobe sakalavae* shows the following combination of features: alveolar channels nearly vertical as in theropods and some terrestrial crocodylomorphs such as "sphenosuchians", baurusuchians, peirosaurids, and sebecosuchids; fused and highly sculpted interdental plates very similar to those of the abelisaurids in shape and texture, and forming an alveolar medial surface flatter than usual in crocodylomorphs; dental foramina resembling those of the Crocodylomorpha in shape, density, and distribution; maxillary medial shelf crocodylomorph in shape (with the exception of the "protosuchians"), similar to the shelf in "sphenosuchians" or alternatively in mesoeucrocodylians, different from that in spinosaurid theropods, and more extended medially than in any other theropod dinosaur; maxillary medial shelf higher to the tooth row than in crocodylomorphs we examined; shape and position of the broad depression on the palate where occlusal contact occurs with the large mandibular teeth recalling the peirosaurid crocodylomorphs (usually more laterally placed in theropods); rostral teeth U-shaped in cross-section as in tyrannosauroid theropods; lateral teeth even more labiolingually inflated than usually found in ziphodont crocodylomorphs and in tyrannosaurid theropods (rounded cross-sections are commonly present in the teeth of the non-ziphodont crocodylomorphs and spinosaurid dinosaurs); tooth crowns stout and relatively short, as usual in crocodylomorphs; smallest lateral teeth globe-shaped (the smallest teeth in Theropoda are usually scaled version of the largest ones) as in several crocodylomorphs (in which, however, they usually have a distinct neck); theropod-like carinal variation; very large autapomorphic tooth denticles, even larger respect to TCH than the largest ones in the large-bodied theropods and considerably larger than the fine denticles of any other ziphodont crocodylomorph. Taking into account this combination of features, *Razanandrongobe sakalavae* clearly appears as a new taxon, but its definitive attribution to the Crocodylomorpha or Theropoda cannot be supported (Fig. 10). For this reason, we refer our material to Archosauria incertae sedis, pending more complete material.

**Paleobiology**

Both theropods and ziphodont crocodylomorphs with nearly vertical maxillae
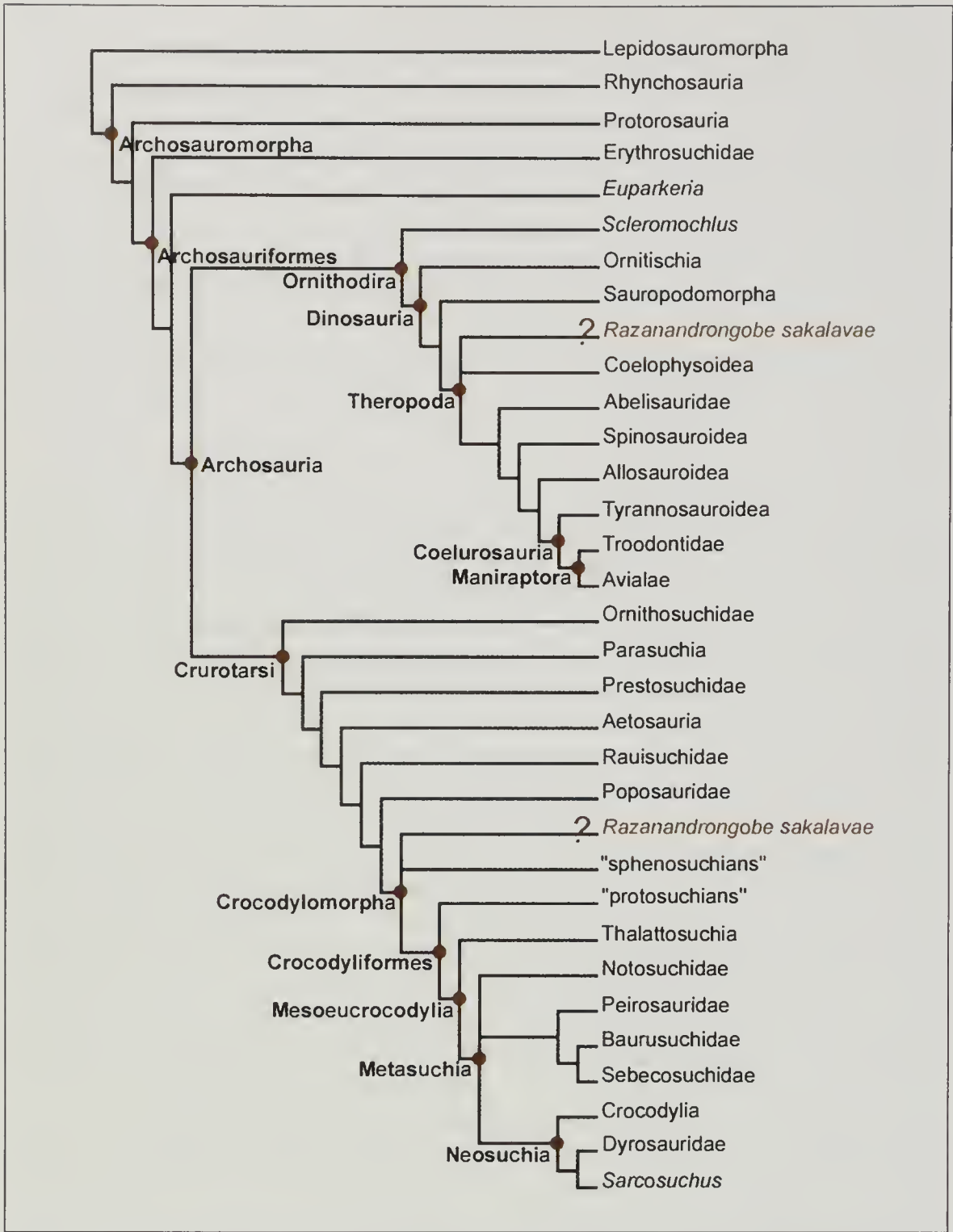
Fig. 10 – Phylogenetic relationships among the archosauromorph taxa cited in the discussion, based mainly on the trees published by Brochu (2001). Additional information about the relationships among basal Crurotarsi and mesoeucrocodylians are taken respectively from Parrish (1993) and Sereno *et al.* (2001). The two hypothetic positions of *Razanandrongobe sakalavae*, marked by a question mark, are represented as unresolved polytomies at the base of Theropoda and Crocodylomorpha.

Fig. 10 – Relazioni filogenetiche tra gli arcosauromorfi citati nella discussione. Schema elaborato principalmente sulla base degli alberi pubblicati da Brochu (2001). Le informazioni addizionali inerenti le relazioni tra i crurotarsi basali e i mesoeucoccodrilli sono tratte rispettivamente da Parrish (1993) e Sereno *et al.* (2001). Le due ipotetiche posizioni di *Razanandrongobe sakalavae*, contrassegnate da un punto interrogativo, sono riportate come politomie irrisolte alla base di Theropoda e Crocodylomorpha.

come from deposits that clearly indicate a terrestrial environment. In this regard, *Razanandrongobe sakalavae* does not represent an exception. A size-comparison between the maxilla and teeth of *R. sakalavae* and other large archosauriform predators clearly demonstrates that it was indeed a very large animal, surpassing by far the size of the other known Middle Jurassic Malagasy predators (Maganuco *et al.*, 2005), and being potentially large enough to feed on the sympatric sauropods (Buffetaut, 2005) such as *Lapparentosaurus* and *Archaeodontosaurus*. The thickness of the bone and the size of the alveoli of MSNM V5770 are comparable to those of the neosuchian *Sarcosuchus* and the tyrannosaurid theropods *Daspletosaurus* and *Tarbosaurus* (pers. obs. 2004). According to Shubert & Ungar (2005), the wear surfaces on the teeth of *R. sakalavae* (see description and Fig. 8H, I) appear closer to ante-mortem enamel spalling caused by tooth-food contact rather than to attritional facets related to tooth-tooth contact. According to Currie *et al.* (1990), it appears verisimilar that flakes of enamel were splayed off the underlying dentine surfaces during traumatic events that occurred as the animal bit into the bones or other hard objects. D. Tanke and P. Currie (pers. comm. 2004) showed us that a similar type of wear has been found in an average of one tooth out of ten among the isolated theropod teeth in Dinosaur Provincial Park. Although our sample is small and, consequently, its statistical significance limited, it is worth to underline that in *R. sakalavae* five teeth of seven present such a kind of spalled surface. The incisiform rostral tooth referred to *Razanandrongobe sakalavae* closely resembles the tyrannosaurid premaxillary teeth, which were more likely used in scraping meat from bone than in capturing prey (Erickson, 1999; Holtz, 2003). Currie (2000) pointed out that the shape of the tyrannosaurid lateral teeth, which are labiolingually inflated and sub-circular in cross-section, increase their strength. We can infer that also *R. sakalavae* had strengthened lateral teeth, because it had teeth even more inflated labiolingually and rounded in cross-section than tyrannosaurids. Also the denticles of *R. sakalavae* appear very similar to those of tyrannosaurids (Currie *et al.*, 1990) in having many features (e.g. size, shape and basal width) typical of strengthened denticles well adapted to bite into bone.

Additionally, the rounded structure at the base of the junction between neighbouring denticles described in this paper is comparable to the round void present in the tyrannosaurids which, as pointed out by Abler (2001), would have protected the posterior edge of the tooth against the propagation of cracks formed by the junction between neighbouring denticles, distributing forces over an increased area. Following Abler (1997) it cannot be excluded either that the narrow junctions between the denticles griped and held meat fibres, possibly facilitating an infectious bite as in extant monitor lizards. As reported by Langston (1973), the expansion and union of the palatal medial shelves represent a strengthening of the cranial skeleton by acquiring a stronger tubular construction. Busbey (1995) demonstrated that the thickening of the bones and the addition of a secondary palate (even an incomplete one) significantly increase the ability of the snout to withstand both vertical bending and axial torsion. Both massive maxillary medial shelf and thickness of the maxillary bony walls are visible in MSNM V5770. According to Senter (2003) the fused interdental plates create a medial wall

around the teeth, which suggests better resistance to transverse force. In conclusion, on the basis of the data collected it is equally parsimonious to postulate that *Razanandrongobe sakalavae* usually killed its prey or not. What can be inferred for certain is that: *R. sakalavae* had a robust snout; the above mentioned features of the maxilla and dentition strongly suggest a diet including also hard tissues such as bones and tendons.

## Conclusions

The present study demonstrates that a new species of very large, terrestrial, predatory archosaur with a unique combination of maxillary and tooth features lived in Madagascar in the Middle Jurassic. Many features of *Razanandrongobe sakalavae*, gen. et sp. nov., strongly suggest that it fed also on hard tissues such as bones and tendons. Besides the autapomorphic denticles, *R. sakalavae* would possess different autapomorphic, synapomorphic and homoplasic features according to which taxon it is compared with. Although *R. sakalavae* differs in some aspects from any currently known member of the Crocodylomorpha and Theropoda, it belongs certainly to one of those two taxa. The nature of our material renders impossible to perform a real phylogenetic analysis, thus at present no one of the two phylogenetic assignments hypothesized above can be definitively confirmed or refuted. Therefore we refer our material to Archosauria incertae sedis.

## Acknowledgements

## References

Abler W. L., 1997 - Tooth Serrations in Carnivorous Dinosaurs. In: The Encyclopedia of Dinosaurs. Currie P. J. & Padian K. (eds). *Academic Press*, New York: 740-743.

Abler W. L., 2001 - A kerf-and-drill model of tyrannosaur tooth serrations. In: Mesozoic Vertebrate Life. Tanke D. H. & Carpenter K. (eds.). *Indiana University Press*: 84-89.

Alcober O., 2000 - Redescription of the skull of *Saurosuchus galilei* (Archosauria: Rauisuchidae). *Journal of Vertebrate Paleontology*, 20 (2): 302–316.

Allain R., 2002 - The discovery of megalosaur (Dinosauria: Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. *Journal of Vertebrate Paleontology*, 22: 548-563.

Benton M. J., 1986 - The Late Triassic reptile Teratosaurus- a rauisuchian, not a dinosaur. *Palaeontology*, 29: 293-301.

Benton M. J. & Walker A. D., 2002 - *Erpetosuchus*, a crocodile-like basal archosaur from the Late Triassic of Elgin, Scotland. *Zoological Journal of the Linnean Society*, 136: 25-47.

Besairie H., 1936 - Recherches géologiques à Madagascar, première suite. La Géologie du Nord-Ouest. *Mémoires Academie Malgache Tananarive*, 21.

Besairie H., 1972 - Géologie de Madagascar. I. Les Terraines Sédimentaires. *Annales Géologiques de Madagascar*, 35: 1-465.

Boast J. & Nairn A. E. M., 1982 - An outline of the geology of Madagascar. In: The ocean basins and margins. Vol. 6. The Indian Ocean. Nairn A. E. M. & Stehli F. G. (eds.). *Plenum Press,* New York: 649-696.

Bonaparte J. F., 1986 - Faunal change across the Triassic - Jurassic boundary. In: The beginning of the age of dinosaurs. Padian K. (ed.). *Cambridge University Press*, New York: 247-258.

Brochu C. A., 1999 - Phylogeny, systematics, and historical biogeography of Alligatoroidea. *Society of Vertebrate Paleontology*, Memoir 6.

Brochu C. A., 2001 - Progress and future directions in archosaur phylogenetics. *Journal of Paleontology*, 75: 1185-1201.

Brochu C. A., 2003 - Osteology of *Tyrannosaurus rex*: Insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Society of Vertebrate Paleontology*, Memoir 7: 1-138.

Buckley G. A., Brochu C. A., Krause D. W. & Pol D. 2000 - A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. *Nature*, 405: 941-944.

Buffetaut E., 2005 - A new sauropod dinosaur with prosauropod-like teeth from the Middle Jurassic of Madagascar. *Bulletin de la Société Géologique de France*, t. 176, n° 5: 467-473.

Busbey A. B., 1995 - The structural consequences of skull flattening in crocodilians. In: Functional Morphology in Vertebrate Paleontology. Thomason J. J. (ed.). *Cambridge University Press*: 173-192.

Campos D. A., Suarez J. M., Riff D. & Kellner A. W. A., 2001 - Short note on a new Baurusuchidae (Crocodyliformes, Metasuchia) from the Upper Cretaceous of Brazil. *Boletim do Museu Nacional, Geologia*, 57: 1-7.

Candeiro C. R. A., Abranches C. T., Abrantes E. A., Avilla L. S., Martins V. C., Moreira A. L., Torres S. R. & Bergqvist L. P., 2004 - Dinosaurs remains from western São Paulo state, Brazil (Bauru Basin, Adamantina Formation, Upper Cretaceous). *Journal of South American Earth Sciences*, 18: 1–10.

Carr T. D., 1999 - Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria). *Journal of Vertebrate Paleontology*, 19 (3): 497-520.

Carroll R. L., 1988 - Vertebrate Paleontology and Evolution, *WH Freeman & Co.*.

Carvalho I. S., Ribeiro L. C. B. & Avilla L. S., 2004 - *Uberabasuchus terrificus sp. nov.*, a New Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. Gondwana Research, 7 (4): 975-1002.

Clark J. M., 1994 - Patterns of evolution in Mesozoic Crocodyliformes. In: In the Shadow of the Dinosaurs. Fraser N. C. & Sues H.-D. (eds.). *Cambridge University Press*: 84-97.

Clark J. M., Sues H.-D. & Berman D. S., 2000 - A new specimen of *Hesperosuchus agilis* from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs. *Journal of Vertebrate Paleontolology*, 20: 683-704.

Clark J. M. & Sues H.-D., 2002 - Two new basal crocodylomorph archosaurs from the Lower Jurassic and the monophyly of the Sphenosuchia. *Zoological Journal of the Linnean Society*, 136: 77-95.

Colbert E. H., 1946 - *Sebecus*, representative of a peculiar suborder of fossil Crocodilia from Patagonia. *Bulletin of the American Museum of Natural History*, 87: 217-270.

Currie P. J., 2000 - Theropods from the Cretaceous of Mongolia. In: The Age of Dinosaurs in Russia and Mongolia. Benton M. J., Shishkin M. A., Unwin D. M., & Kurochkin E. N. (eds.). *Cambridge University Press*: 434-455.

Currie P. J., 2003 - Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. *Acta Palaeontologica Polonica*, 48 (2): 191-226.

Currie P. J., Rigby J. K. Jr. & Sloan R. E., 1990 - Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: Dinosaur Systematics: Perspectives and Approaches. K. Carpenter K. & Currie P. J. (eds.). *Cambridge University Press*, New York: 107-125.

Dal Sasso C. & Pasini G., 2003 - First record of pterosaurs (Pterosauria, Archosauromorpha, Diapsida) in the Middle Jurassic of Madagascar. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano*, 144 (II): 281-296.

Dal Sasso C., Maganuco S., Buffetaut E. & Mendez A. M., 2005 - New information on the skull of the enigmatic theropod *Spinosaurus*, with remarks on its size and affinities. *Journal of Vertebrate Paleontology*, 25 (4): 888-896.

Erickson G. M., 1999 - Breathing life into *Tyrannosaurus rex*. *Scientific American*, 281: 42-49.

Flynn J. J., Parrish J. M., Simpson W. F., Razafimanantsoa L., Andriatompohavana R. & Totovolahy A., 1997 - New Triassic and Jurassic Vertebrates from Madagascar. *Journal of Vertebrate Paleontology*, 17 (3, suppl.): 46A.

Flynn J. J., Parrish J. M., Rakotosaminanana B., Simpson W. F. & Wyss A. R., 1999 - A Middle Jurassic mammal from Madagascar. *Nature*, 401: 57-60.

Galton P. M., 1985 - The poposaurid thecodontian *Teratosaurus suevicus* v. Meyer, plus referred specimens mostly based on prosauropod dinosaurs, from the middle Stubensandstein (Upper Triassic) of Nordwürttemberg. *Stuttgarter Beiträge zur Naturkunde, Serie B*, 116: 1-29.

Gasparini Z., Chiappe L. M. & Fernandez M., 1991 - A new Senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous crocodilians. *Journal of Vertebrate Paleontology*, 11 (3): 316-333.

Gomani E. M., 1997 - A crocodyliform from the Early Cretaceous Dinosaur Beds, Northern Malawi. *Journal of Vertebrate Paleontology*, 17 (2): 280-294.

Gow C. E., 2000 - The skull of *Protosuchus haughtoni*, an Early Jurassic crocodyliform from southern Africa. *Journal of Vertebrate Paleontology*, 20 (1): 49-56.

Gower D. J. & Sennikov A. G., 2000 - Early archosaurs from Russia. In: The Age of Dinosaurs in Russia and Mongolia, Benton M. J., Shishkin M. A., Unwin D., and Kurochkin E. N. (eds.). *Cambridge University Press*, Cambridge: 120-139.

Gradstein F. M., Ogg J. G. & Smith, A. G., (eds.), 2004 - A Geologic Time Scale 2004. *Cambridge University Press*.

Holtz T. R. Jr., 2000 - A new phylogeny of the carnivorous dinosaurs. *Gaia*, 15: 5-61. (The papers of the December 1998 issue of Gaia are technically dated 2000).

Holtz T. R. Jr., 2001a - The phylogeny and taxonomy of the Tyrannosauridae. In: Mesozoic Vertebrate Life. Tanke D. H. & Carpenter K. (eds.). *Indiana University Press*, USA: 64-83.

Holtz T. R. Jr., 2001b - Pedigree of the tyrant kings: New information on the origin and evolution of the Tyrannosauridae. *Journal of Vertebrate Paleontology*, 21 (3): 62A-63A.

Holtz T. R. Jr., 2003 - Dinosaur Predation. Evidence and ecomorphology. In: Predator-Prey Interactions in the fossil record. Kelley P. H., Kowalewsky M., & Hansen T. A. (eds.). *Kluwer Academic/Plenum Publishers*, New York: 325-340.

Hurum J. H. & Sabath K., 2003 - Giant theropod dinosaurs from Asia and North America: Skulls of *Tarbosaurus bataar* and *Tyrannosaurus rex* compared. *Acta Palaeontologica Polonica*, 48 (2): 161-190.

Hutt S., Naish D., Martill D. M., Barker M. J. & Newbery P., 2001 - A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. *Cretaceous Research*, 22: 227-242.

Janensch W., 1925 - Die Coelurosaurier und Theropoden der Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica* 1(Suppl. 7): 1-99.

Juul L., 1994 - The phylogeny of basal archosaurs. *Palaeontologia Africana*: 1-38.

Kellner A. W. A. & Campos D. A., 2002 - On a theropod dinosaur (Abelisauria) from the continental Cretaceous of Brazil. *Arquivos do Museu Nacional*, 60 (3): 163-170.

Langston W., 1973 - The crocodilian skull in historical perspective. In: Biology of the Reptilia, 4. Gans C. & Parson T. S. (eds.). *Academic Press*, New York: 263-284.

Langston W., 1975 - Ziphodont crocodiles: *Pristichampsus vorax* (Troxell), new combination, from the Eocene of North America. *Fieldiana Geology*, 33: 291-314.

Lavocat R., 1955 - Etude des gisements de dinosauriens de la region de Majunga (Madagascar). *Travaux du Bureau Géologique*, 69: 1-19.

Lehman T. M. & Carpenter K., 1990 - A partial skeleton of the tyrannosaurid dinosaur *Aublysodon* from the Upper Cretaceous of New Mexico. *Journal of Paleontology*, 64: 1026-1032.

Lydekker R., 1895 - On bones of a sauropodous dinosaur from Madagascar. *Quarterly Journal of the Geological Society of London*, 51: 329-336.

Maganuco S., Cau A. & Pasini G., 2005 - First description of theropod remains from the Middle Jurassic (Bathonian) of Madagascar. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano*, 146 (II): 165-202.

Motani R., 1997 - Temporal and spatial distribution of tooth implantation in ichthyosaurs. In: Ancient Marine Reptiles. Callaway J. M. & Nicholls E. L. (eds.). *Academic Press*: 81-103.

Nash D. S., 1975 - The morphology and relationships of a crocodilian, *Orthosuchus stormbergi*, from the Upper Triassic of Lesotho. *Annals of South African Museum*, 67 (7): 227-329.

Ogier A., 1975 - Etude de nouveaux ossements de Bothriospondylus (Sauropode) d'un gisement du Bathonien de Madagascar. Doctoral thesis (3ᵉ Cycle), Universitè Paris VI.

Ortega F. & Gasparini Z., 2000 - A new species of *Araripesuchus* (Crocodylomorpha, Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina). *Journal of Vertebrate Paleontology* 20 (1): 57-76.

Parrish J. M., 1993 - Phylogeny of the Crocodylotarsi, with reference to archosaurian and crurotarsan monophyly. *Journal of Vertebrate Paleontology*, 13: 287-308.

Pol D., 2003 - New remains of *Sphagesaurus huenei* (Crocodylomorpha: Mesoeucrocodylia) from the Late Cretaceous of Brazil. *Journal of vertebrate Paleontology*, 23 (4): 817-831.

Prasad G. V. R. & de Lapparent de Broin F., 2002 - Late Cretaceous crocodile remains from Naskal (India): comparisons and biogeographic affinities. *Annales de Paléontologie*, 88: 19-71.

Rauhut O. W. M., 2003 - The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology*, 69: 1-213.

Sampson S. D., Witmer L. M., Forster C. A., Krause D. W., O'Connor P. M., Dodson P. & Ravoavy F., 1998 - Predatory dinosaur remains from Madagascar: Implications for the Cretaceous biogeography of Gondwana. *Science*, 280: 1048-1051.

Schubert B. W. & Ungar P. S., 2005 - Wear facets and enamel spalling in tyrannosaurid dinosaurs. *Acta Palaeontologica Polonica* 50 (1): 93-99.

Senter P., 2003 - New information on cranial and dentary features of the Triassic Archosauriform reptile *Euparkeria capensis*. *Palaeontology*, 46 (3): 613-621.

Sereno P. C., 1991 - Basal archosaurs: phylogenetic relationships and functional implications. *Society of Vertebrate Paleontology*, Memoir 2: 1-53.

Sereno P. C., Beck A. L., Dutheil D. B., Gado B., Larsson H. C. E., Lyon G. H., Marcot J. D., Rauhut O. W. M., Sadleir R. W., Sidor C. A., Varricchio D. J., Wilson G. P. & Wilson J. A., 1998 - A long-snouted predatory dinosaur from Africa and the evolution of Spinosaurids. *Science*, 282 (5392): 1298-1302.

Sereno P. C., Larsson H. C., Sidor C. A. & Gado B., 2001 - The Giant Crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science*, 294: 1516-1519.

Sereno P. C., Wilson J. A. & Conrad J. L., 2004 - New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proceedings of the Royal Society of London*, B: 1471-2954.

Stromer [von Reichenbach], Ernst. 1914. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 1. Einleitung und 2. *Libycosuchus*. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-Physikalische Klasse, München*, 27 (3): 1-16.

Sues H.-D., Shubin N. H., Olsen P. E. & Amaral W. W., 1996 - On the cranial structure of a new protosuchid (Archosauria: Crocodyliformes) from the McCoy Brook Formation (Lower Jurassic) of Nova Scotia, Canada. *Journal of Vertebrate Paleontology*, 16 (1): 34-41.

Thevenin A., 1907 - Paléontologie de Madagascar. IV Dinosauriens. *Annales de Paléontologie*, I (II): 121-136.

Walker A. D., 1972 - New light on the origin of birds and crocodiles. *Nature*, 137: 257-263.

Walker A. D., 1990 - A revision of *Sphenosuchus acutus* Haughton, a crocodylomorph reptile from the Elliot Formation (late Triassic or early Jurassic) of South Africa. *Philosophical Transactions of the Royal Society of London, Biological Sciences*, 330: 1-20.

Weishampel D. B., Dodson P. & Osmólska H., (eds.), 2004 - The Dinosauria. Second Edition. *University of California Press*.

Willis P. M. A. & Mackness B., 1996 - *Quinkana babarra*, a new species of ziphodont mekosuchine crocodile from the Early Pliocene Bluff Downs Local fauna, Northern Australia, with revision of the genus. *Proceedings and Journal of the Linnean Society of New South Wales*, 116: 143-151.

Wu X.-C. & Chatterjee S., 1993 - *Dibothrosuchus elaphros*, a crocodylomorph from the Lower Jurassic of China and the phylogeny of the Sphenosuchia. *Journal of Vertebrate Paleontology*, 13 (1): 58-89.

Wu X.-C. & Russell A. P., 2001 - Redescription of *Turfanosuchus dabanensis* (Archosauriformes) and new information on its phylogenetic relationships. *Journal of Vertebrate Paleontology*, 21 (1): 40-50.

Zaher H. & Rieppel O., 1999 - Tooth Implantation and Replacement in Squamates, with Special Reference to Mosasaur Lizards and Snakes. *American Museum Novitates*, 3271: 1-19.

Zinke J., 1998 - Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). *Palaontologische Zeitschrift*, 72 (1/2): 179-189.